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Fishes of the Gulf of Maine, by Henry B. Bigelow and William C. Schroeder. Washington, viii - 577 pp., 1953. Photo-offset reprint, $6.50.

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No. 1 — *Gular Musculature in Delphinids*[1]

By Barbara Lawrence and William E. Schevill

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[1] Contribution No. 1437 from the Woods Hole Oceanographic Institution

GULAR MUSCULATURE IN DELPHINIDS

INTRODUCTION

A scattering of authors in the past ninety years have published on different aspects of the head and throat musculature in the odontocetes. No two have gone about their dissections in the same way, the names used for the muscles vary, and in some instances the inadequacy of their material has led to conflicting statements on the number and position of the muscles involved. Our investigations of sound production in the larynx have pointed up the need for a series of more detailed dissections of the entire region, as well as for correlating the descriptions of some of these early workers with each other and with the conditions that we actually found.

Our primary concern has been to establish the true relationships of the hyo-laryngeo-pharyngeal muscles or, to put it differently, to study the muscles which lie between the throat cartilages and the base of the cranium, medial to the basioccipital plates and posterior to the palate. Whether or not the great development of the basioccipital plates is related to the peculiar structures associated with the ear bones or to the evolution of an intranarial larynx, the combined result has been a characteristic arrangement of the muscles in this region which is common to many odontocetes. Since accurate dissection of these deeper layers depends on an understanding of the more superficial ones, the latter also have been figured and described. The muscles external to the pterygoid plates are quite distinct from those of the throat region, and so are omitted. The boundary between these two regions is a tough, fibrous membrane which extends from the tip of the pterygoid hamulus to the tissue investing the bulla on each side, and lies across the notch in the pterygoid plates. It separates the muscles of the bony nares from the pterygoid muscles. The complex of air sinuses and retia external to this has been well described by Fraser and Purves (1960a, pp. 65-68).

The first section of this paper deals with four rather closely related genera represented by the following species: *Delphinus delphis* Linné 1758, *Stenella plagiodon* (Cope) 1866 and *S. styx* (Gray) 1846, *Tursiops truncatus* (Montagu) 1821, and *Lagenorhynchus acutus* (Gray) 1828 and *L. albirostris* Gray 1846. Herein they will usually be referred to by generic name only. The purpose of this section has been not to compare the four genera, but to establish the common delphinid arrangement of muscles in this region. For this reason, the dissections have rarely duplicated each other. Most of the figures are of *Delphinus,* but to show certain details some figures of *Tursiops* and some of *Lagenorhynchus* are included. The specimens studied are those reported on in the "Functional anatomy of the delphinid nose" (Lawrence and Schevill, 1956), and include, in addition, a specimen of *Lagenorhynchus albirostris* and one of *Stenella styx,* as well as a representative of the Phocoenidae, *Phocoena phocoena* (Linné) 1758, all collected in the western North Atlantic.

The second section is a clarification of Murie's classic description of the throat region in *Globicephala melaena* (Traill) 1809. Although also a delphinid, this is a much larger form which differs further from the above four genera in its relatively shorter rostrum and broader skull.

In the following, for ease of description, the muscles considered are grouped and discussed in three divisions: the superficial layers, the muscles of the neck and throat, and the pharyngeal muscles.

GENERAL ACCOUNT OF DELPHINIDAE

In the hope of standardizing muscle names in the cetaceans, we have not followed one author but have selected what seem to us the most appropriate terms. Huber's terminology (1934, pp. 117-119) has been used for the superficial layers. For the hyo-laryngeo-pharyngeal region, the names are chiefly from Murie (1873), Kernan and Schulte (1918), and Howell (1927). When the names used are Latin adjectival forms, the word "*musculus*" is to be understood as preceding the name; when the adjectives are anglicized, the English word "*muscle*" may be understood to follow the name.

In order to avoid confusion between the bones and similarly named muscles, we have followed Howell (1927) and earlier authors in using the "-hyal" ending for different components of the hyoid apparatus, as for instance thyrohyal, while in these cases we have used "-oid" for muscles, as for instance *thyrohyoid.* Since the thyro- and basihyal elements fuse early, it is not possible to tell whether certain muscles attach on both or on only one or the other. This is an unimportant detail; nevertheless, it should be remembered that in some instances what we call a thyrohyal attachment may really be a thyrobasihyal attachment and vice versa. The current names for the laryngeal cartilages are so universally accepted that the standard forms thyroid, cricoid, and arytenoid have been used. This is less confusing than in the case of the hyoid apparatus, for in the larynx parallel names for muscles are not in common use.

To make clear the interrelationship of the muscles as well as to compare better our findings with those of other workers, the material was actually dissected in a number of different ways. The sequence in which the muscles are presented here is chosen as the easiest for purposes of identification, as they are exposed in progressively deeper ventrolateral dissection. Additional details of the more complicated muscles based on other types of dissection are also illustrated. These are essential if function as well as identification is to be understood.

Aside from Murie's work on *Globicephala*, the most useful of the earlier dissections of this region in odontocetes have been made by: Schulte and Smith (1918), and Kernan and Schulte (1918) of *Kogia*; by A. B. Howell of *Neomeris* (1927), and Boenninghaus of *Phocoena* (1902); by Fraser and Purves of *Delphinus* (1960a and b); and by Hein (1914) of *Monodon*. Where our dissections overlap and their findings differ significantly from ours, these are discussed; otherwise their work is merely noted.

Superficial Layers

Huber's (1934, pp. 117-120, fig. 4) detailed description of the facial muscles of *Tursiops*, published posthumously, is an integral part of his carefully reasoned series on the evolution of facial musculature. In another paper (Lawrence and Schevill, 1956), we have discussed his account of the blowhole musculature in the light of our own findings. His description of the superficial facial muscles matched closely what we observed in the four genera dissected, and the following comments are mainly supplementary. These outer layers have been considered by us only because of their relation to the deeper hyopharyngeal regions which are our primary concern.

The blubber in the region of the head and throat is closely bound to the underlying muscle. Some of the outermost layers of the *sphincter colli* actually insert in the dense inner layers of the blubber. Ventral to the eye and surrounded by the *sphincter colli profundus*, *auriculolabialis*, and *orbicularis oris*, there is an extensive area of fat lying directly beneath the blubber and against the jaw. The remnant of the outer ear lies buried in this. Distally, this vestige is a very slender tube surrounded by dense fibrous tissue and embedded in fat. Proximally, the tube widens and is partially enclosed by small, curved cartilages of a characteristic shape.

M. sphincter colli profundus (Fig. 1, *spf*). This extends in a thin, transverse sheet from the symphysis of the jaw to the region behind the flipper, beyond which it was not dissected. This muscle was studied only in *Delphinus* and *Lagenorhynchus acutus*. In these, an aponeurotic area occurs on the throat over the *sternohyoid*. Posterior to this, especially laterally between the forelimb and the ear, the *sphincter colli profundus* is thicker. Along each side, at about the level of the eye, it meets the *sphincter colli primitivus*. Dorsal to the forelimb, from the line where these two meet, a small bundle of fibers converges to insert in the flipper. Anterior to this, a very few fibers pass ventrally to attach to the fibrous mass surrounding the auditory tube, and deep to these a few other fibers merge with those of the *auriculolabialis*.

M. sphincter colli primitivus (Fig. 2, *spt*). This lies dorsal to the *sphincter colli profundus* and is very difficult to distinguish from it along the line where the two meet. Only a slight difference in the direction of the fibers suggests that, instead of a single thin sheet of muscle wrapping around the side of the face and throat, there are in reality two muscles. A small, doubtfully distinct, anterior segment (Fig. 2) attaches in the dense fibrous tissue investing the slender tube which passes from the minute orifice of the outer ear to the vestigial ear cartilages. This may be what Huber (1934, p. 117) refers to as "a small vestige of the extrinsic postauricular musculature." This is the only part of *sphincter colli primitivus* figured.

M. auriculolabialis (Figs. 1, 2, *al*). This arises mainly along the rim of the zygomatic process of the squamosal external to the glenoid fossa and posteroventral to the root of the zygomatic arch. Posteriorly, it is partly overlain by the ear cartilage, and a small part of the muscle takes origin in the tissue here. From its origin, *auriculolabialis* passes anteriorly, ventral to *orbicularis oculi*, diminishing rapidly in size, to insert as described later. The primary squamosal origin is fairly constant in all the forms dissected, but the origin of the thin layer which is associated with the vestiges of the outer ear varies. In *Delphinus* this is in the fibrous mass surrounding the auditory tube, distal to the cartilage; in *Stenella plagiodon* it is diffusedly in the tissue investing the ear cartilage itself, while in *Lagenorhynchus acutus* there is no apparent connection with the cartilage, but the attachment is in the connective tissue mass between cartilage and skull. The relation of the insertion of *auriculolabialis* to *orbicularis oculi,* the zygomatic arch, and the connective tissue beneath the latter varies. In *Delphinus* and *Stenella plagiodon* we found *auriculolabialis* inserting in part on the arch itself, while in *Lagenorhynchus acutus* the insertion was in the connective tissue ventral to the arch. In all three there was a certain connection with *orbicularis oculi*, very slight in the last genus, more definite in the two former. In *Tursiops,* Huber says that *auriculolabialis* passes from the preauricular region to fuse with *orbicularis oculi* and gives no other insertion for it. Possibly all of this is individual, not generic, variation and an indication that *auriculolabialis* in delphinids is degenerating. This muscle is the *tympano-zygomaticus* of Howell (1927, p. 22).

M. orbicularis oculi (Fig. 2, *oc*). We dissected this in detail only in *Stenella plagiodon*. Here, as in Huber's *Tursiops*, it forms a well-developed sphincter around the eye. A few of the outer fibers anteriorly and posteriorly attach to the margin of the orbit, while anteroventrally some pass downward into fibrous fatty tissue between the eye and *orbicularis oris.*

M. orbicularis oris (Fig. 2, *or*). This is a weak and very fat muscle whose fibers radiate from the connective tissue near the corner of the mouth and end in the fibrous inner layer of blubber.

M. nasolabialis (not figured). The muscles between the eye and the melon were dissected in detail only in *Stenella plagiodon* and did not match Huber's figure of *Tursiops* (1934, fig. 4A, p. 118). In this region, he shows a single rather extensive *nasolabialis* continuous with the anteriormost fibers of *orbicularis oculi.* The situation in *Stenella* was a little different; here we found two small sheets of fibers which were separated from the *orbicularis oculi* by the maxillary bone. The more posterior took origin on a narrow area on the maxillary, dorsal to the anterior part of the eye, and passed anteriorly to end in the fibrous mass beneath the melon. The more anterior sheet arose in front of this, possibly on the lacrymal as well as the maxillary, and passed anterodorsally to end in the same region as the posterior. Both are poorly developed and no attempt has been made to decide of which layers they are vestiges.

Ear muscles (Fig. 2). These were not dissected out in detail, but an apparently single small muscle was found beneath the *sphincter colli primitivus* with fibers directed anteroventrally to insert in the fibrous tissue on the inner side of the upper end of the ear cartilage and surrounding the slender auditory tube.

Huber (1934, pp. 134-35, fig. 11) gives a thorough account of the ear muscles in *Monodon,* and Murie (1873, p. 250, fig. 29) discusses them in *Globicephala.* Fraser and Purves (1960a, p. 62) refer to them rather generally in the course of a more detailed account of other aspects of the ear.

Discussion. Huber's identification of the muscles in this region is built on evolutionary studies which have led him to the conclusion that the *platysma* and the *sphincter colli profundus* derive from the *sphincter colli primitivus.* In cetaceans he recognizes both the *primitivus* and *profundus,* but says that the *platysma colli et faciei* is lacking. Earlier authors have tended to include the superficial musculature of the head and neck in the *panniculus carnosus* (Murie, 1873, figs. 57, 58; Howell, 1927, p. 19; Schulte and Smith, 1918, p. 15). Though Murie (1873, pp. 272, 273) refers to the anterior portion as the *platysma,* the others do not make such a distinction. The dorsoventral division into a *sphincter colli primitivus* and *profundus* emphasized by Huber does not show in their figures. This separation, though not very definite in our dissections, is still sufficiently apparent to reinforce Huber's opinion. Kesteven (1941, pp. 74-75), while recognizing the same muscle arrangement as that found by Huber and ourselves, believes that *sphincter colli primitivus* and *profundus* are actually anterior extensions of the *panniculus carnosus* and do not belong to the superficial facial musculature.

Schulte and Smith's description (1918, pp. 14-15) of the *sphincter colli* musculature (called *panniculus carnosus*) in *Tursiops* does not entirely match Huber's and our dissections. Their aponeurotic area on the throat anterior to the *pectoralis* is as we found it. We differed, however, in not finding, on the side of the neck immediately anterior to the forelimb, an aponeurotic layer with which the ventral aponeurosis was continuous. On the contrary, in this region the muscle was well developed, passing ventrally across the *sternohyoid,* in part to join its fellow, in part to end at the *pectoralis.* Posterior to this and dorsal to the forelimb, there is a distinct separation between the thicker band of fibers passing anterior to the forelimb and the thinner layer which converges to insert on the forelimb. The development of an aponeurosis in this area may vary individually; we found it only in *Lagenorhynchus acutus,* and here it was always separated from the aponeurotic throat patch by the flipper.

Huber's derivatives of the *sphincter colli profundus* — the *auriculolabialis* (*tympano-zygomaticus*), *orbicularis oculi,* and *orbicularis oris* — were all found by Howell. It is probable that the "bundles" of Schulte and Smith (1918, p. 14) "caudal to the angulus oris" are the same as the *orbicularis oris.*

MUSCLES OF THE NECK AND THROAT

The muscles described in this group are ventral only, and for the most part associated with the hyoid apparatus. The more superficial and anterior are described first under the heading of interramal and tongue muscles, the more posterior and deeper are described second under the heading of hyoideal muscles.

Correlated with the development of a fusiform body, the neck in cetaceans has been shortened and thickened and the muscles of the throat strongly developed. The hyoid elements also are well developed, with their main portions ossified even in young animals. In adult individuals, the basi- and thyrohyals form a single, broadly crescentic bone extending across the throat for the full width between the basicranial plates. Anteriorly on each side, a cartilaginous ceratohyal connects each basihyal with a three-sided, rod-like stylohyal, which is also ossified. The stylohyal attaches to the exoccipital by means of a cartilaginous tip which may be a separate element and is sometimes called the tympanohyal.

Functionally, the expanded hyoid apparatus is important as an attachment for a number of muscles in this region, where the typical cetacean relation of jaw and occipitals makes a more standard mammalian arrangement impossible. The *digastric* or *depressor mandibulae* has its origin here, and a very thick *sternohyoid* helps to fix the basi-thyrohyals in place as the jaw is opened. Counteracting this backward pull is a moderately strong *geniohyoid* and the much expanded *interhyoid* which draws the thyrohyal up and forward towards the stylohyal, while the latter is in turn lifted by the *palatopharyngeus.*

The association of the tongue muscles with the hyoid apparatus is a more normal one and needs little comment here.

Interramal and Tongue Muscles

The muscles of the interramal region and the tongue are easy to distinguish and not too different from those of other mammals.

Mylohyoid muscle (Figs. 2, 8, *my*). This is a thin, coarsely fibered, transverse muscle that covers the throat from the symphysis of the jaw to the hyoid region. Anteriorly, a few of the more external fibers insert in the tough membrane along the lower margin of the jaw, while the main mass of the muscle turns upward to insert in the tissue internal to the lower part of the jaw. Posteriorly, the muscle passes between the *geniohyoid* and the *digastric,* becoming increasingly fat towards its insertion, with the *digastric,* in the fatty tissue inside the jaw. Here, the direction of the fibers is dorsal and slightly posterodorsal, and the transition from muscle to fat mass is so gradual that it is not possible to say where the one ends and the other begins. This is characteristic of the *digastric* as well. The connection with the hyals is vestigial and lateral only. Here, on each side, a thin sheet of the *mylohyoid* passes internal to the *digastric* to attach with it via the same aponeurotic sheet on the thyrohyal. Medial to this, the *mylohyoid* ends in an aponeurosis which merges with that attaching the *geniohyoid* to the basihyal. Anterior to this aponeurosis, the fibers of each side meet in an ill-defined raphe which is bound, in the midline, to the *geniohyoid.* In *Stenella plagiodon,* the anterior portion of the *mylohyoid* was difficult to separate from the overlying *sphincter colli profundus.*

The *mylohyoid* is identified as such by Schulte and Smith, Howell, and Hein. Boenninghaus figures but does not discuss it.

Digastric muscle (Figs. 2, 3, 8, 9, *d*). This arises chiefly from the thyrohyals and probably in part from the basihyal also; laterally, a few fibers take origin along a ligament which runs from the tip of the thyrohyal to the tissue investing the tympanohyal cartilage. The *digastric* becomes increasingly more fatty as it passes anterodorsally to terminate in the fatty tissue around the lower margin of the jaw. The same gradual transition from muscle to fat seen in the *mylohyoid* makes it not possible to define exactly the insertion of the *digastric.* Generally speaking, it is around the posterior third of the jaw. Some variation in the exact direction of the fibers showed in the different individuals dissected.

The *digastric* of this paper is the same muscle as Schulte and Smith's *hyomandibularis* and Howell's *monogastric.* Hein's *digastric,* although figured at insertion only, is clearly the same as ours.

Geniohyoid muscle (Figs. 3, 8, *gh*). Situated between the *digastric* muscles and internal to the *mylohyoid,* this muscle is very distinct from the underlying complex of tongue muscles, from which it is separated by sheets of loose connective tissue. It takes origin in an aponeurosis across the basihyal external to the *hyoglossus* and internal to the *mylohyoid* muscles. As described above, the aponeurotic insertions of both *mylohyoid* and *geniohyoid* are closely bound together. The belly of the muscle is thick and rather short and the insertion is in a long, rather thick aponeurosis inside the jaw at the symphysis. A few of these tendinous fibers are also closely bound to the *mylohyoid.*

Some variation was noted in the different forms dissected. In *Delphinus,* its origin extended a little distance on to the thyrohyal where it was overlaid by the insertion of the *digastric* and its insertion was on the inner surface of each ramus of the jaw as well as at the symphysis. In *Stenella plagiodon* and *Lagenorhynchus acutus* there is no overlap of *digastric* and *geniohyoid* at their origin. For the most part this appeared to be a single muscle, though in *Lagenorhynchus acutus* the proximal end of the belly internally showed a slight separation into two parts.

Schulte and Smith show and describe (1918, fig. 11, p. 37) a *geniohyoid* which is much like ours; in their figure 12, page 39, the origin shown for the *genioglossus* is probably that of the *geniohyoid.* Howell describes a *geniohyoideus* which differs from ours in taking origin along the entire cranial borders of the basihyal instead of transversely across the middle, and suggests that the insertion is in the tongue, not the mandible. His figures (1927, fig. 4, p. 10, fig. 9, p. 25) of the *geniohyoid,* showing an extensive thyro- as well as a basihyal origin, look more like our *hyoglossus.*

Hein found no *geniohyoid,* but does not take this as proof of its absence in *Monodon.* In his specimen only the hyoid attachments of the superficial throat muscles were left, and here, as described above, the aponeurotic attachments of *mylo-* and *geniohyoid* are one. For this reason, we agree with Hein's supposition that a *geniohyoid* does occur in *Monodon,* and further believe that it is much like the *geniohyoid* found in our dissections.

The *geniohyoid* is figured but not discussed by Boenninghaus.

M. styloglossus (Figs. 3, 4, 8, 9, *sg*). This muscle has its origin on the anterior surface of the lateral end of the stylohyal, dorsal to the attachment of the *interhyoideus*. It is characteristically thick at its origin, often bluntly wedge-shaped with the wide end lateral, and the tapering end sometimes extending along as much as a third of the length of the stylohyal. From its origin it passes anteriorly, ventral to the *hyoglossus* and dorsal to the *genioglossus* to insert in the under surface of the tongue anterior to, and in part also lateral to, the medial part of the *hyoglossus*. Where the two meet at their insertion, they mingle. Schulte and Smith, Howell, and Hein all find a *styloglossus* which differs little from ours.

M. hyoglossus (Figs. 4, 8, 9, *h*). This is a paired muscle, that of each side being indistinctly divided into two sections (Figs. 3, 8). Its origin laterally is from the anterior border of the thyrohyal between the *mylohyoid* and *interhyoid*, and medially from the basihyal (processus lingualis) internal to the *geniohyoid*. From its origin the muscle passes forward between the *styloglossus* and *palatoglossus*, radiating in a thin layer of coarse fibers to surround the oropharynx almost completely. The lateral section, which is also the most posterior, inserts on the dorsal surface of the *palatoglossus*. The medial section sends a few thin bundles to the sides of the oropharynx, but for the most part passes internal to the *genioglossus* to mingle with the *styloglossus* at its insertion in the under surface of the tongue. The degree of distinctness of the two parts varied in the genera examined.

The *hyoglossus* of Schulte and Smith as well as that of Howell is clearly the same as ours, although they differ in certain respects. The former is described as a smaller muscle with origin from the ceratohyal. The latter is said to have its origin on stylo- and ceratohyal; this may be an error, as Hein in *Monodon* and we, as well as Boenninghaus, in *Phocoena*, found the attachment of the *hyoglossus* to be much as in the Delphinidae. Hein's *hyopalatinus* is the lateral portion of our *hyoglossus*.

M. genioglossus (Figs. 3, 4, 8, 9, *gg*). This muscle lies internal to the *geniohyoid* and takes its origin medially in a long raphe from the ventral surface of the tongue and pharynx. From its origin it passes anterolaterally, spreading over the insertions of *hyoglossus* and *styloglossus* to insert principally in the lining of the anterior part of the buccal cavity. A few fibers also mingle with the *mylohyoid* to insert in the lower inner margin of the jaw posterior to the *geniohyoid*. At its caudal end, a narrow, scarcely muscular band of the *genioglossus* lies internal to the hyals, with which it has almost entirely lost its connection. In *Tursiops,* a vestigial connection remains, via a thin aponeurotic sheet, to the dorsal surface of the basihyals as well as to the dorsal surface of the *geniohyoid*. While our failure to find such a connection in the other three genera does not mean it is necessarily always absent, the primary posterior insertion of the *genioglossus* is medially in the ventral wall of the pharynx. Where the *palatoglossus* wraps around the pharynx, the origin of the *genioglossus* is from the ventral surface of the *palatoglossus,* while anterior to this it is in the root of the tongue. *M. genioglossus* is not always clearly distinct at its origin, and, in *Lagenorhynchus acutus* at least, where the lateral section of the *hyoglossus* inserts on the *palatoglossus,* parts of the three mingle so as to be indistinguishable from each other.

Schulte and Smith as well as Howell find a similar *genioglossus.* Boenninghaus' *genioglossus* s. s. (1902, p. 66, pl. 1, fig. 1) and the anterior part of Hein's *genioglossus* are homologous with our muscle.

In addition, Boenninghaus describes a posterior extension of the *genioglossus* which he calls the *genioepiglotticus.* Boenninghaus describes and figures this (1902, p. 66, pl. 1, fig. 1) as a medial, ventral band of muscle passing from the pharynx to the epiglottis. This in effect would bind the wall of the pharynx to the epiglottis anteroventrally. We found no such connection. Posteroventrally, the tongue muscles end with the insertion of *palato-* and *genioglossus* (Fig. 8). Caudal to this, the pharynx passes dorsal to the cerato- and basihyals and divides to go between the epiglottid and thyroid cartilages on each side (Fig. 6). In this region, as described under *palatopharyngeus*, there is a continuity of muscle from pharynx to epiglottis. This, however, is lateral and posterior to the division of the pharynx. Medially, where the pharynx divides, the larynx is strongly bound to the hyals by the *hyoepiglotticus* (see below) but this muscle is quite distinct from the pharyngeal muscles.

Boenninghaus further distinguishes a *glossoepiglotticus* which he says goes from the dorsal surface of the base of the tongue and merges with *genioepiglotticus* (1902, p. 66, pl. 1, fig. 1). In our dissection of *Phocoena* a careful search was made for both of these muscles. Only two extrinsic muscles were found inserting on the anterior part of the epiglottis, the *hyoepiglotticus* and the anterior portion of the thyropalatine section of the *palatopharyngeus*. The arrangement of these did not significantly differ from that found in the Delphinidae.

In both groups, posterior to the margin of the *palatoglossus*, where the pharynx lies dorsal to the hyoid complex, there is a well defined non-muscular area. Anterior to this are the muscles of the oropharynx; posterior to this are the muscles of the hyoid apparatus and the nasopharynx. Along the lateral walls of the divided pharynx, a few fibers (see under *palatoglossus*) pass between these two regions. They have no connection with the *hyoepiglotticus*, from which they are separated by a distinct space. Whether these belong to the *palatopharyngeal* complex or to that of the tongue muscles, or whether they are vestiges of totally other muscles is not clear. In any event, they are so poorly developed as to have little functional significance.

Hein (1914), apparently following Boenninghaus, also describes a complex *genioglossus*, distinguishing a posterior portion of this as the *genioepiglotticus*. Where he figures this as medial (pl. 5, fig. IX, muscle 54), we believe this to be an error, though possibly it could be part of our *hyoepiglotticus*. Where he figures it as lateral (fig. X, muscle 54), it is apparently a better developed part of what we describe below as a posterior extension of the combined *palato-* and *genioglossus*. Muscle 67 of figure X, also called *genioepiglotticus*, appears to be part of the thyropalatine section of our *palatopharyngeus*. Hein, like us, was unable to identify a *glossoepiglotticus*.

M. palatoglossus (Figs. 4, 6, 8, 9, *pg*). This surrounds the oropharynx for almost its entire length, and mingles without sharp boundary with the various tongue muscles which lie external to it, the *hyoglossus* laterally and the *genioglossus* ventrally. Dorsally, the *palatoglossus* is closely bound to the bony palate, and in the midline fibers from opposite sides meet, but do not form a conspicuous raphe. For the most part, the *palatoglossus* is here thinly covered by the lateral section of the *hyoglossus*, although anteriorly it extends beyond this latter. From the posterior margin of the combined *palatoglossus* and *genioglossus* a very few fibers extend, as described above, along the lateral walls of the divided pharynx to join a similarly indistinct section of the *palatopharyngeus*. As stated earlier, this fiber tract is probably what Hein has called *genioepiglotticus*. It may also include the *glossoepiglotticus* of Boenninghaus.

Schulte and Smith have no muscle corresponding to this, but Howell, Hein, and Boenninghaus all report a *palatoglossus* which, except as described above, is the same as ours.

Hyoideal Muscles

Identification of those muscles which fix the position of the hyoid relative to the sternum, and those muscles which fix the position of the larynx relative to both the sternum and hyoid apparatus presents no serious problems. Although their arrangement differs in certain characteristic ways from that in other mammals, homologies are not difficult to understand.

With the deeper layers the situation is different. The great transverse extension of the thyrohyal bone and the rather narrow space separating the thyrohyal from the stylohyal bones have resulted in rearrangement of the muscles of this region. A single large mass, presumably equivalent to the *cerato-hyoideus* (=*interhyoideus*) of other mammals, fills the whole interspace between these two. Of the two other muscles usually found in this region, the *stylohyoideus* and *occipitohyoideus* (=*jugulohyoideus*), there is only one vestigial remnant. The attachments of this small muscle differ from both of the above, and whether or not it is the displaced homologue of either, it is not possible at this time to say. From its position, we tend to believe it is the *occipitohyoid* and have so called it.

Sternohyoid muscle (Figs. 1, 2 *sh*). This is a thick muscle arising on the anterior part of the sternum, and covering the thyroid cartilage medially as it passes forward to insert broadly on the basi- and thyrohyal bones.

There is little disagreement over the name of this muscle although, by misprint, Howell (1927, p. 26) calls it as well as the next muscle *sternothyroideus*.

Sternothyroid muscle (Fig. 4, *st*). This arises on the anterior margin of the sternum and, in *Stenella plagiodon* at least, from the first rib near its sternal attachment. Thence it passes anteriorly to insert on the outer surface of the posterior horn of the thyroid. Schulte and Smith (1918, p. 39), reversing Howell's error, call this as well as the foregoing muscle *sternohyoid*.

Thyrohyoid muscle (Fig. 4, *th*). This is a thin, paired muscle lying ventral to the strong aponeurotic sheet which connects the thyroid and epiglottid cartilages. The *thyrohyoid* takes origin on the side of the thyroid cartilage anterior and ventral to the insertion of the *sternothyroid.* Thence it passes anteriorly and a little ventrally, crossing the ventral part of the thyroid insertion of the *occipitothyroid,* to insert on the posterior margin of the basihyal and on the posteromedial border of the thyrohyal as well. In some instances as in *Lagenorhynchus acutus,* there is a well developed fibrous sheet across the angle between these two, to which the *thyrohyoid* also attaches.

Schulte and Smith, Howell, and Hein all identify this same muscle.

Occipitohyoid muscle (Figs. 3, 8, *oh*). This is a thin, small muscle which has its origin behind the bulla in the region of the cartilaginous tip (sometimes called tympanohyal) of the stylohyal, whence it passes ventrally across this cartilage to insert on the dorsal tip of the thyrohyal. There is some variation in exact origin, as the stylohyal and the exoccipital are closely bound together and invested with tough fibrous tissue which also covers the bulla. In *Delphinus* and *Lagenorhynchus acutus,* the origin was from this tissue where it overlay the stylohyal. In *Tursiops,* we found it in the tissue between the stylohyal and the bulla.

Schulte and Smith (1918, pp. 36, 37, and 38) describe a *depressor mandibulae* which they homologize with the *occipitohyoideus* of Rapp and Stannius. According to them it has its origin in the dense fibrous tissue in the region of the articulation of the jaw and inserts in the tip of the hyoid (=thyrohyal) continuously with the *mylohyoid.* Undoubtedly this is the homologue of our muscle, although the *mylohyoid* in our dissections did not extend this far laterally, and the origin of our *occipitohyoid* was more posterior. Boenninghaus (1902, pp. 61-63, fig. S) describes and figures this muscle, which he considers to be homologous with the *hyopharyngeus* or *constrictor medius.* Neither Howell nor Hein mention such a muscle.

Interhyoid muscle (Figs. 3, 4, 8, *ih*). This paired muscle fills the space between the hyal bones on each side. It arises from most of the dorsal surface of the thyrohyal as well as anterodorsally on the basihyal, and passes anterodorsally to insert around the posterior surfaces of stylo- and ceratohyals. Medially, the two muscles are separated by the *hyoepiglotticus.* The lateral extent of the stylohyal insertion of the *interhyoid* shows some variation. In *Lagenorhynchus acutus* and *Delphinus*, a small portion attached ventral to the origin of the *styloglossus;* in *Stenella plagiodon* the attachment was more medial with almost no overlap with the *styloglossus.*

Schulte and Smith call this muscle *ceratohyal* or *hyoideus latus*, Howell calls it *ceratohyoideus*, and Hein uses *hyostylohyoideus* but gives *interhyoideus* as a synonym. Boenninghaus does not refer to it.

M. hyoepiglotticus (Figs. 5, 6, *he*). This is a strong, single muscle. Its origin medially on the dorsal surface of the basihyal separates the left and right *interhyoid;* it is long anteroposteriorly, but rather narrow. In *Stenella plagiodon* and *Lagenorhynchus acutus*, its origin extends also onto the ceratohyal, where it is dorsal to the *interhyoid*. From its origin the fibers pass posteriorly and a little ventrally to insert on the anterior surface of the epiglottid cartilage about one-third of the distance up from its base. Ventral to this muscle between the posterior border of the basihyal and the lower part of the epiglottis is a strong ligament.

Kernan and Schulte describe a double *hyoepiglottic* muscle, while Howell and Hein both find it single. Boenninghaus figures but does not describe a *hyoepiglotticus* which looks like ours.

Muscles of the Pharynx

In order that the arrangement of the pharyngeal muscles in the odontocetes be understood, the relation of the hyoid apparatus and the laryngeal cartilages to each other and to the skull needs to be discussed further. In these mammals the larynx is permanently intranarial. Consequently, it lies close to the base of the skull and to the posterior bony nares, into which the arytenoepiglottid cartilages protrude (Fig. 10).

While the thyroid cartilage lies posterior to the thyrobasihyals, the much elongated arytenoepiglottids pass anterodorsally internal to the hyoid apparatus, between the basioccipital-pterygoid plates and into the nares. These plates, which extend on each side from the exoccipital to the bony nares, project ventrally as flanges between the basicranial region medially and the bulla and prebullar region laterally. This is a typically odontocete arrangement, as is a corresponding ventral development of the exoccipital posterior to the bulla. Whether or not this modification is primarily to help to isolate the bulla acoustically from the throat region is of peripheral interest for the moment. The significant thing is that, coincident with these changes, the tympanohyal has shifted its cranial attachment to the exoccipital behind the bulla, and as the exoccipital has moved ventrally, so also has the stylohyal. The shift has also moved the thyrohyal too far ventrally to articulate with the thyroid. Such an articulation is further made impossible by a transverse development of the flattened thyrobasihyals so great that this complex spans the space between the basioccipital plates (basioccipital crests of Fraser and Purves, 1960b, p. 24, fig. 7; p. 25, fig. 8). The thyroid cartilage, no longer supported by the hyals, is directly attached to the base of the skull by strongly developed paired lateral muscles, the *occipitothyroids*.

Further rearrangements of the muscles of the pharyngeal region are caused by the fact that the pharynx, instead of passing dorsal to the larynx, divides in front of the *hyoepiglotticus* to pass on each side of this muscle and the elongated arytenoepiglottid cartilages (Fig. 10). It passes between these cartilages and the horns of the thyroid on each side and forms a single passage again posterior to the arytenoepiglottids and internal to the *occipitothyroid* muscle. This arrangement of the pharynx, the position of the hyals, and the attachment of the thyroid to the base of the skull effectively isolate the pharynx from any hyal attachments of the constricting muscles.

The bones and cartilages of the base of the skull are not the only structures that have been modified by the requirements of an aquatic existence. Because of the permanently intranarial position of the larynx, the functions of those pharyngeal muscles which are often called constrictors differ from those of other mammals. Primarily, in the odontocetes, they are concerned with holding the larynx in place in the bony nares. This is accomplished in two ways: by means of a sphincter around the tip of the arytenoepiglottid cartilages, and by drawing the larynx up and forward into the back of the bony nares. Of the muscles involved, two, the *palatopharyngeus* and the *pterygopharyngeus*, hold the larynx in place by means of a powerful sphincter. A third muscle in this region, the *occipitothyroid*, binds the larynx firmly to the ventral surface of the skull. The only muscle that has a sole constricting function is the *thyreopharyngeus*. Because of these changes, and without a detailed study of innervation, it has not been possible to homologize with any degree of certainty the muscles of this region with those of other mammals. For instance, the sphincter muscle of the posterior nares was found to be made up of two main units, called here the *pterygopharyngeus* and *palatopharyngeus* and very probably homologous with those of other mammals. The same is true of the *thyreopharyngeus*, which might be found to include the *cricopharyngeus*. Whether or not the two parts of the *hyopharyngeus* are represented by the entirely differently placed *occipitothyroid* is uncertain.

Two other mammalian muscles normally found in this region, the *tensor* and *levator palati*, are either missing or much modified because the soft palate as such has ceased to exist in the Delphinidae, and their function is obsolete. Instead, there extends posterior to the hard palate, for a short distance, a thickened aponeurosis. This is called by some authors (e.g. Kernan and Schulte, 1918) the velum palati; we have followed Fraser and Purves (1960a and b) in calling it the palatine aponeurosis. From its dorsal surface the *palatopharyngeus* takes origin in part. Laterally, from the tips of the pterygoids to the tissue investing the bulla the palatine aponeurosis is continued as the pterygoid ligament.

M. stylopharyngeus (Figs. 6, 7, 9, *sp*). This muscle takes origin narrowly on the dorsomedial side of the stylohyal near its cranial articulation and expands somewhat as it passes anterodorsally across the *palatopharyngeus*, to mingle with it and the ventral border of the *pterygopharyngeus* at its insertion in the lateral walls of the nasopharynx. It follows closely the course of the eustachian tube which opens into the nares internal to the insertion of the *stylopharyngeus.*

Both Schulte and Smith (1918, pp. 38-39) and Kernan and Schulte (1918, p. 261) describe a similar *stylopharyngeus.* Howell gives no details of this postnarial region. Fraser and Purves (1960a, p. 68, fig. 85; 1960b, p. 21, fig. 6) call this the *levator palati.*

Boenninghaus describes and figures (1902, pp. 45-47, pl. 1, fig. 3) a *stylopharyngeus* in *Phocoena* with styloid origin as in our *stylopharyngeus*, but with the two parts joined and lying ventral to the pharynx. This does not agree with our dissection of *Phocoena*, in which the *stylopharyngeus* is paired, and, except for being less distinct from the *pterygopharyngeus* at its insertion, resembles closely that of the Delphinidae. Lack of knowledge of the Delphinidae and the fact that *stylo-* and *pterygopharyngeus* in *Phocoena* are more completely merged in the walls of the pharynx have probably led Boenninghaus to a mistaken identification of the distal ends of these two muscles. His figure 3 of plate 1, which purportedly illustrates this region, has certain errors which are further confusing and are discussed in more detail below.

M. palatopharyngeus (Figs. 4-7, 9, *pp*, *ppt*). The *palatopharyngeus* as identified here is both complex and not well defined. It is a very thick muscle which has its origin over a large area extending from the anteromedial wall of the bony nares to the pterygoid margin of the palate and across the narrow palatine aponeurosis to the pterygoid ligament and stylohyal. Within the nares (Fig. 9), its attachment is principally on the pterygoids posterior to the vomer and on each side of a raphe which extends from the vomer to the margin of the palate and separates the two halves of the muscle. At its dorsal margin, the *palatopharyngeus* mingles, with no sharp boundary, with the ventral margin of the *pterygopharyngeus* (Fig. 9). For this reason, it is hard to define exactly the extent of the insertion of each on pterygoid and palatal bones. From its origin, part of the *palatopharyngeus* sweeps more or less horizontally around the tip of the arytenoepiglottid cartilages in a strong sphincter (Figs. 7, 9), the outer layers joining those of the *thyreopharyngeus* in the mid-dorsal region. Some pass beneath the *thyreopharyngeus* to join, via tendinous bands, the fibers of the opposite side; a few end on top of the *thyreopharyngeus*. A second part, consisting of the innermost layers of the *palatopharyngeus*, forms the *arcus palatopharyngeus*. A third part of the *palatopharyngeus*, called the *pars thyropalatinus*, passes posteroventrally to insert between the thyroid and epiglottid cartilages.

While the main mass of the muscle is internal, it can be understood best in detail if we examine it as it shows in progressively deeper lateral dissections. When the thyrohyal bone and its attached muscles are cut away, the thyropalatine section of the *palatopharyngeus* may be seen attaching on the laryngeal cartilages in the region where the oropharynx divides to pass around the arytenoepiglottid cartilages (Fig. 5). Its exact insertion varies somewhat in the genera examined. In *Delphinus*, it is on the lower half of the inner surface of the thyroid cartilage, the adjacent part of the pharynx and the lower part of the epiglottid cartilage, with only the suggestion of a division between the epiglottid and more dorsal portions. In *Stenella* *plagiodon* the insertion is distinctly double. The posterior part is on the pharynx and on the inner face of the body of the thyroid in a narrow vertical band extending ventrally from the anterior border of the notch. The anterior and also more ventral insertion is between the thyroid and the epiglottid, chiefly on the former, but with a few strands to the latter. In *Lagenorhynchus albirostris* there are two separate thyroid attachments as in *Stenella plagiodon*, although the muscle is not double. The intervening fibers insert in the tissue between the epiglottid and thyroid cartilages. In this genus attachments to the wall of the pharynx are poorly developed.

From the anterior border of the thyropalatine portion of the *palatopharyngeus* a few fibers (not figured) pass forward between the *interhyoid* and the wall of the pharynx, which here lacks muscle fibers. Some of these fibers end on the dorsal surface of the *interhyoid*, to which they are loosely bound by connective tissue. Anterior to this and somewhat more dorsally, a few fibers extend on top of the combined *genio-* and *palatoglossus*. This is the portion of the *palatopharyngeus* referred to in our discussion of *genioglossus*.

From its laryngeal insertions, in all three genera, the *thyropalatine* portion of the muscle widens as it passes anterodorsally towards the posterior bony nares. A posterior segment of the external portion attaches (Figs. 5, 7) strongly to the stylohyal; anterior to this, the external layers pass internal to the stylohyal (Figs. 5, 6), to which they are loosely bound by connective tissue, and attach to the pterygoid ligament. Deep to these external *thyropalatine* layers, but not distinct from them, the main mass of the *palatopharyngeus* (Fig. 7) passes up the bony nares internal to the *stylopharyngeus*.

If the skull is so cut away that the nasopharynx can be laid open along the midline posteriorly and its mucous membrane dissected away from the underlying muscle, this latter is observed as a single mass indistinctly divisible on the basis of texture and direction of fibers. By far the greatest bulk of this muscle is made up of rather coarse, anteromedially directed fibers which are the combined *palato-* and *pterygopharyngeus;* in this inner aspect there is no real separation between the two. In the midline anteriorly are paired raised bundles of a more finely fibered layer which is probably Boenninghaus' *pars interna* of the *palatopharyngeus*. At their upper end the fibers of this layer are as coarse as and indistinguishable from the underlying *pterygopharyngeus* with which it mingles as the two converge laterally towards the opening of the eustachian tube. At their lower end the paired bundles separate to encircle the arytenoepiglottid spout in a strong sphincter muscle, which also is more finely textured than the more external layers with which it merges. In its pharyngeal aspect this sphincter, the *arcus palatopharyngeus*, is separated laterally from the overlying muscle by deep pockets. The coarser mass external and lateral to the sphincter is probably what is sometimes called the *pars externa* of the *palatopharyngeus* which medially, in part, passes ventral to the *pars interna* to insert in the raphe which is closely attached to the wall of the bony nares.

In *Kogia*, Kernan and Schulte (1918, pp. 261-262) describe a *palatopharyngeus* which includes all of the component parts found in our dissections, although they do not separate a *pars interna* or *externa*. What we have called a *thyropalatine* portion, they refer to as the "superficial portion of the palato-pharyngeus." Their emphasis on the unity of this muscle is equally applicable to our dissections. In their *palatopharyngeus* the blending with *pterygopharyngeus* at the insertion of *stylopharyngeus*, the involvement in the *arcus palatopharyngeus*, and origin from velum and pterygoid all parallel the situation in the delphinids. Differences, which include a band of fasciculi passing beneath our *thyreopharyngeus*, as well as no mention of any stylohyal attachments, are surprisingly slight between families with such markedly unlike crania.

In *Delphinus*, Fraser and Purves' *palatopharyngeus pars interna* and *externa* (1960b, pp. 17-22, figs. 3-6) passes up the nares as does our *palatopharyngeus* and is probably the same as our muscle, although in their figure 3 the ventral portion, in a somewhat misleading fashion, appears to wrap around the ventral surface of the larynx. Hein's discussion of the pharyngeal region is incomplete, but his *constrictor pharyngeus superior* is our *palatopharyngeus*.

Comments on Boenninghaus' work will come at the end of this section.

M. pterygopharyngeus (Fig. 9, *ptp*). This muscle lies dorsal to the *palatopharyngeus* and together with it surrounds the tip of the larynx. Its origin is from the anterior wall of the upper part of each bony naris. When the nasopharynx is removed from the bony nares and the external arrangement of the muscles examined, the *stylopharyngeus* is seen partially to separate the *pterygo-* and *palatopharyngeus* laterally.

The *pterygopharyngeus* passes outward as well as postero-ventrally to meet its fellow of the opposite side in an ill-defined raphe in the mid-dorsal line of the nasopharynx. Posteriorly, in the midline, it is separated from the *thyreopharyngeus* and the transverse fibers of the *palatopharyngeus* by a small aponeurosis. When the lining of the nasopharynx is removed, no separation between *palato-* and *pterygopharyngeus* is found.

Boenninghaus distinguishes a small paired, medial muscle overlying the *pterygopharyngeus* dorsally, which he calls the *salpingopharyngeus*. We found no such distinct layer in this region, although, at its dorsal insertion, the most posterior fasciculus of the *pterygopharyngeus* was distinct for a few millimeters. Internally, when the mucous lining was removed, a faintly differentiated longitudinal bundle of slightly finer fibers was observed. This rather finer bundle gradually merged distally and externally with the surrounding coarser fibers and was quite distinct in direction as well as structure from the ventral, internal fiber bundle identified earlier as Boenninghaus' *pars interna* of the *palatopharyngeus*. Further comments on Boenninghaus will come at the end of this section, and are applicable also to Fraser and Purves, who follow Boenninghaus.

Kernan and Schulte describe a *pterygopharyngeus* which closely resembles ours. Neither Howell nor Hein deal with the nasopharynx.

Occipitothyroid muscle (Figs. 4-7, 9, *ot*). This strong muscle draws the thyroid cartilages, and thus the whole larynx, up towards the base of the skull. Its outer portion has its origin in the fibrous tissue in the region of the bulla and on the margin of the basioccipital plate anterior to the hypoglossal canal. Thence its inner portion extends broadly across the basioccipital to meet its fellow of the opposite side. Its insertion is on the external surface of the anterior horn of the thyroid cartilage and on the adjacent walls of the pharynx. Details appear to vary in the genera examined, though the main plan is as described above. In *Delphinus* and *Lagenorhynchus albirostris* some of the posterior fibers wrap around the pharynx, passing on top of the *thyreopharyngeus* in so doing. In *Tursiops* a small slip also takes origin on the tip of the stylohyal cartilage. In *Stenella plagiodon* the outer and inner sections seem somewhat more distinct at their origins. Parallel dissections were not made of each genus, so that complete comparative comments are not possible.

In Schulte and Smith (1918, fig. 11, p. 37) the muscle labeled *inferior constrictor* is probably the outer part of our *occipitothyroid;* in Kernan and Schulte (1918, p. 260) it is the rostral portion of the *inferior constrictor* (*thyreopharyngeus*) which is equivalent to our *occipitothyroid.* The attachment on the thyroid cartilage is the same, but there is no mention of any cranial attachment. This is the muscle called by Boenninghaus *laryngopharyngeus* seu *constrictor pharyngis inferior* (1902, pp. 59-61). Fraser and Purves (1960b, pp. 20, 21, 137, fig. 6) identify this muscle as the *constrictor pharyngeus* or *superior constrictor* muscle.

M. thyreopharyngeus (Figs. 5-7, 9, *tp*). This muscle takes origin on the posterior horn of the thyroid cartilage and passes anterodorsally across the pharynx, medial and internal to the *occipitothyroid.* The thyroid origin of this muscle is the principal one in all four genera examined. In *Delphinus* the origin extends across the cricothyroid articulation as well, and in *Lagenorhynchus albirostris* a few fibers medial to this take origin on the circular layer of the oesophagus. From its origin, the *thyreopharyngeus* passes anteromedially across the circular muscle of the oesophagus and the *palatopharyngeus* to meet the *pterygopharyngeus.* In *Delphinus* and *Lagenorhynchus albirostris,* an inscriptio intervenes between the insertion of the *pterygo- and thyreopharyngeus,* though not in *Tursiops* and *Stenella plagiodon.*

This is the muscle identified by Kernan and Schulte (1918, p. 260) as the caudal portion of the *inferior constrictor* (*thyreopharyngeus*). Interpreting Boenninghaus' text and figures in the light of our dissections of *Phocoena* as well as of the Delphinidae, it seems clear that his *longitudinalis oesophagi* is the same as our *thyreopharyngeus.* He gives an anterior cranial attachment for this which we did not find, and which does not seem possible in view of the way the *occipitothyroid* passes dorsal to the *thyreopharyngeus* in this region. Hein's *constrictor inferior pharyngeus* is probably the same as our *thyreopharyngeus,* although it is too incompletely described for certainty.

Homologies with Phocoena. Boenninghaus in his careful work (1902) on the pharynx in *Phocoena* makes a diligent effort to find and identify the various muscles found in land mammals, especially man. This emphasis on homology leads to the recognition of more layers than are apparently distinct in the delphinids, and is one of the reasons why he found it impossible to relate his work to Murie's and to Macalister's on *Globicephala*. Our dissection of *Phocoena* showed an arrangement of the pharyngeal muscles very similar to that found in the delphinids, and one which did not always match Boenninghaus' plates.

For this reason Boenninghaus' discussion of the pars superior of the pharynx needs to be considered in some detail. In his introductory comments, Boenninghaus himself emphasizes that the muscle of the pars superior is essentially a single mass (1902, pp. 38-41), exactly as we found it to be. If this is not kept well in mind, his subsequent division of it into as many parts as he does is misleading.

Primarily, he identifies a constrictor of the pars superior pharyngis which he says is made up of three distinct muscles in terrestrial mammals: the *pterygopharyngeus*, *palatopharyngeus* (*pars externa* and *interna*) and the *thyreopalatinus*. We consider the *pterygopharyngeus* to be better developed than does Boenninghaus, and restrict the *palatopharyngeus* to the more ventral part of this musculature. This discrepancy between the limits of his *pterygo-* and *palatopharyngeus* and ours stems from his effort to separate the two on the basis of pterygoid or palatal attachments. Since the relationship of these bones in *Phocoena* is different from that in the delphinids, while the relationship of the two sections of muscle is much the same in both, it is better to follow an apparent though slight natural division in the muscle mass itself.

In the phocoenids, the palatal bones intervene medially between the pterygoids and extend to the rim of the bony palate, but in the delphinids these bones are broadly separated from the margin of the bony palate by the pterygoids. Thus, if identification were to be based on muscle attachment only, the positions of *pterygo-* and *palatopharyngeus* would be reversed between delphinids and *Phocoena*. Actually, as described above, a distinct though not pronounced separation between the two muscles (Fig. 9) occurs approximately at the level of the insertion of *stylopharyngeus*. Since in other mammals (cf., Sisson, 1917, p. 407) the *stylopharyngeus* inserts in the wall of the pharynx between *pterygo-* and *palatopharyngeus*, the separation is best made here. Thus the more posterior part of our *pterygopharyngeus* is equivalent to part of Boenninghaus' *pars externa* of *palatopharyngeus*, as well as his associated *salpingopharyngeus*.

While it is possible to correlate Boenninghaus' *pterygo-, palato-* and *thyreopharyngeus* with the muscles observed by us in *Phocoena,* his text and especially his figures for *salpingo-* and *stylopharyngeus* and the *levator veli* are confusing. If his figure 3 (pl. 1, 1902) is an anterior, slightly ventral view with the oropharynx cut away at the entrance to the sinus pyriformis, then the *stylopharyngeus* is wrongly identified; the medial muscle anteroventral to the epiglottis is the *pars externa* of the *palatopharyngeus* which, lateral to its insertion on the dorsal surface of the palatine aponeurosis, attaches also to the stylohyal. The *stylopharyngeus* lies dorsal as well as a little lateral to this and follows the course of the eustachian tube into the bony nares. At its upper end its course is much like that figured by Boenninghaus (1902, fig. 3, no 2) for *salpingopharyngeus.* We found that the *stylopharyngeus* of *Phocoena* differs from that of the Delphinidae in merging more completely with *pterygopharyngeus,* so that it was impossible to tell, in the region of the eustachian tube, which slips were *pterygo-* and which *stylopharyngeus.*

At its ventral end, Boenninghaus (1902, p. 42) says his *salpingopharyngeus* meets in an inscriptio the *longitudinalis oesphagi* (= our *thyreopharyngeus*). His description of the relation between these two leaves little doubt that his *salpingopharyngeus* is a slip which we could not separate from the main mass of the *pterygopharyngeus* either in the delphinids or in our adult *Phocoena.* As far as its insertion at the mouth of the eustachian tube is concerned, in *Phocoena* the *stylo-* and *pterygopharyngeus* were completely merged in this region. In the delphinids, where the insertion of the *stylopharyngeus* is more discrete, this seems to be the muscle surrounding the opening of the tube.

Boenninghaus' *levator veli* (=*levator palati*) is that part of *pterygopharyngeus* with which the *pars interna* of *palatopharyngeus* merges. The difference in fiber direction as illustrated in his plate 1, figure 2, layers 1 and 3, does not indicate distinct layers, but, as shown in our dissections, merely a gradual curving around and converging of a single muscle mass towards its dorsal insertion. At the mouth of the eustachian tube we did not find the discrete insertion figured by Boenninghaus. For these reasons, as well as because Boenninghaus himself emphasizes the lack of separation of the muscles he discusses in this region, we have not considered *levator veli* to be a separate muscle. No *tensor veli* (= *tensor palati*) as described by Boenninghaus was found. Fraser and Purves, although generally following Boenninghaus, do not agree with his identification of the *tensor palati* and believe (1960b, pp. 11, 19, fig. 4) that it lies lateral to the pterygoid bones and thus external to the area with which the present paper deals.

Discussion

The highly specific modifications of the gular region in the odontocetes are for the most part centered around changes in form and in position of the larynx, changes that are directly related to the needs of an aquatic environment. The advantages of an intranarial larynx in terms of underwater feeding are apparent; to what extent either the intranarial position or the form of the larynx is also an advantage in phonation is not yet explained. In any event the laryngeal cartilages both enclose and pass through the pharynx instead of lying for the most part ventral to it. The elongated arytenoepiglottid cartilages, on each side of which the oropharynx passes, have already been described. Ventral, as well as anterior to these, lie the posteroventrally extended palatal and pterygoid bones. A deep air sinus divides these into inner and outer laminae, the inner forming the anterior wall of the bony nares while the outer extends the roof of the mouth and hence the pharynx downward as well as posteriorly almost as far as the larynx. Together these bones separate oro- and nasopharynx. The posterior extension of the palate, such that a purely ventral movement of the larynx cannot disengage it from the posterior bony nares, helps to insure the intranarial position of the larynx. This development of the palate also directs away from the posterior nares the food being swallowed.

The rather complicated rearrangement of the pharyngeal muscles to insure the intranarial position of the larynx may seem confusing in terms of homologies and comparisons with other mammals, but functionally is very simple. The thyroid cartilage, having lost its connection with the thyrohyal, is suspended from the base of the skull by a very strong muscle, the *occipitothyroid*. Lateral to the epiglottis this muscle also draws the walls of the pharynx apart. Anteriorly and quite distinct from this muscle is the *palatopharyngeus*, which lifts the anterior part of the larynx up and forward into the bony nares. The laryngeal attachments on each side are near the ventral part of the larynx, and the muscle passes external to the pharynx.

Both the *occipitothyroid* and the *palatopharyngeus* have an outward as well as an upward pull which insures that the pharynx is not squeezed shut where it passes on each side between the arytenoepiglottids and the thyroid.

In addition to providing a strong muscular connection between the larynx and the skull, part of the *palatopharyngeus* forms a complete sphincter around the expanded tip of the arytenoepiglottids, which further helps to hold the larynx in position in back of the nares.

While the primary function of these muscles has become a supporting one, the *palatopharyngeus* is also involved in shortening the pharynx during swallowing. Contraction of that part of the muscle which has its origin in the anterior wall of the nares and which surrounds the pharynx external to the arcus, not only grasps the arytenoepiglottids more tightly, but it also draws the dorsal wall of the pharynx anteriorly. Posterior to the arytenoepigottids, where the pharynx is again a single passage, the *thyreopharyngeus* is, as usual, a constrictor. The function of the *stylopharyngeus* is to spread the walls of the nasopharynx external to the arcus. It is apparently also involved in opening the eustachian tube.

Powerful as are the muscles holding the larynx in place, there are no opposing muscles to exert the posteroventral force which would be needed to withdraw the larynx from the back of the bony nares. The only laryngeal muscles with a posterior pull are the poorly developed *sternothyroids*. Tension on these spreads the wings of the thyroid cartilage rather than moving the entire larynx. Ventral to the larynx, and also with a posterior pull, lies the strongly developed *sternohyoid*. Tension on this moves the hyals only slightly, with no corresponding shift of the larynx.

Anteriorly, there is only one extrinsic laryngeal muscle, the *hyoepiglotticus*. The action of this is to move the epiglottis away from the arytenoids, thus opening the tip of the larynx. Obviously, when the larynx is opened it will not at the same time be withdrawn from the nares, and the anterior slightly dorsal direction of the fibers from epiglottis to hyals ensures that this will not happen.

Recent authors (Lilly, 1961; Brown, 1962) who have assumed that the larynx in odontocetes can be and is withdrawn from the nares, have done so on the basis of certain phenomena which they wished to explain, and not on the basis of the anatomy involved. Lilly (1961, p. 237), discussing *Tursiops truncatus,* states, "The larynx can also be disengaged from the nasopharynx entirely by the throat muscles connected to the hyoid bone and dropped down in order to discharge water into the mouth from the upper bronchial tree and trachea." Aside from the improbability of such a need, the absence of a thyroid-thyrohyal joint, the lack of a suitable muscle connection between larynx and hyals, and the position of the thyrobasihyals anterior to the larynx, all prevent the muscles acting on the hyoid from moving the larynx with it. Further, the position of the strongly developed *sternohyoid* immediately ventral to the larynx inhibits any downward movement of the larynx, especially when this muscle is contracted as it would have to be if the hyoid were being pulled posteriorly.

In one of his interesting and informative notes on behavior and pathology of captive cetaceans, Brown (1962, pp. 63-64) attributed the death of a captive *Globicephala scammoni* to "laryngeal occlusion induced by inspiration of a stone," although the stone was not found in the animal. It was picked up after having fallen out of the severed head and subsequently interpreted as the cause of a laryngeal lesion. He supposes the following sequence of events: the stone was swallowed; the animal vomited, retracting the larynx as it did so; the stone then passed up into the nasopharynx; the larynx was reinserted in the nasopharynx and the stone inhaled. There are a number of anatomical difficulties with this explanation. The lack of musculature for retracting the larynx has already been discussed. Within the larynx, the paired arytenoids lie very close to each other, and to the epiglottid at their base, narrowing the passage in this region to a slit. When the larynx is opened, this is done by the *hyoepiglotticus,* which separates the cartilages at their tips; there is no additional musculature to enlarge this slit-like passage. Between the epiglottid and the arytenoids at their base, and somewhat ventral to the main air passage, is a distensible pouch. A large object passing down the larynx might lodge here, and it is difficult to see how it could then be moved down the main air passage.

As evidence that laryngeal occlusion has occurred, lesions of the floor and side walls of the larynx in the region of the thyroid are offered. This is the region where the pharynx passes on each side of the arytenoepiglottids, separating the thyroid from the rest of the larynx and trachea. What seems more likely is that the stone, lodged in the pharynx here, may have been responsible for the lesions.

Brown further states that a *Tursiops* whose jaws were forcibly held apart convulsed, vomited, and then expelled vomitus through his blowhole. Though Brown believes this is evidence of laryngeal retraction, it is far more likely that the vomitus was passed up the nares between the sphincter and the arytenoepiglottids, as is anatomically entirely possible for a liquid.

Brown further theorizes that withdrawing the larynx may be a means of facilitating "the passage of large items of food." Actually, even if the larynx is artificially withdrawn from the nares, the length of the arytenoepiglottids is such that they still project across the pharynx (Fig. 11). With the larynx in place, the highly stretchable pharynx on each side of the epiglottis can pass any mass of food that has passed the isthmus faucium and that can be accommodated by the oesophagus. This is possible because of the vertical expansion of the passage and the lateral spread of the horns of the thyroid.

In a dead animal, it is perfectly possible to disengage the tip of the larynx by reaching up the throat and into the nasal passage with the fingers. In a specimen in which the pharyngeal muscles had not been cut, pulling the sternothyroid muscle as strongly as possible either ventrally or posteriorly did not withdraw the larynx from the nares, nor did tilting the larynx force the tip down and so out of the nares.

The possibility of jaw motion moving the larynx was also investigated. The attachments of the *digastric* and other anterior throat muscles to the hyals and the independence of the hyals from the thyroid make this seem unlikely. In addition, prying the jaw of a dead animal open as widely as possible produced no detectable shift in position of the larynx.

Adapted as the musculature of this region is to holding the larynx in place intranarially without interfering with the swallowing mechanism, it is not surprising that the larynx is only with difficulty dislodged. In the absence of any morphological arrangements to accomplish this and since there is no need for the animals to do so, it seems clear that the odontocetes do not voluntarily move the larynx in and out of the nares.[1]

Aside from studying the hyo-pharyngeo-laryngeal region as a functional unit, perhaps the most important result of our dissections has been our ability to reconcile apparently very dissimilar dissections by earlier workers, and to establish that in the five principal odontocete families the arrangement of the muscles and cartilages in this region is remarkably similar. Few

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[1] See note on page 35.

investigators of cetacean anatomy have studied this region in detail. The difficulties involved in the necessary deep dissections have caused most authors, preoccupied as they usually have been with the general anatomy of a particular species, to limit their attention to the more superficial throat and hyoid musculature. Others, who have studied the larynx in detail, have illustrated and described a larynx already severed from the skull.

The most complete account of the throat region in the Delphinidae is still that of *Globicephala* published by Murie some ninety years ago. This is discussed in detail in the second section of this paper. Murie's earlier work on *Lagenorhynchus* (1871) only touches on the region studied here. In this earlier paper, the function of the musculature of the posterior nares is discussed (p. 144), but the individual muscles are not described. Of the hyoid muscles, two are considered in detail, the *hyo-epiglottic* which is the same as ours, and the *hyoideus* which equals our *interhyoid.* Certain other muscles are figured but not described. Of these, his *geniohyoid* (pl. 5, fig. 8) looks like our *genioglossus* and his *genio-hyoglossus* like our *hyoglossus.* We have not been able to identify his *levator palati.* Kesteven's work (1941, pp. 78-79), which treats of some of the tongue and hyoideal muscles in *Delphinus delphis,* is of particular interest in that he describes the innervation of these. His *jugulo-hyoideus* (= our *occipitohyoid*) is supplied by the glossopharyngeal nerve, which supports Boenninghaus' belief that this muscle is homologous with the *constrictor medius* rather than the *digastric.* His *genio-hyoid, genio-glossus,* and *stylo-hyoideus* (= our *interhyoid*) resemble ours. His description and figures of *stylo-glossus* and *hyo-glossus* are reversed; the long narrow muscle which he calls the *hyo-glossus* should have its origin at the end of the stylohyal and is the *styloglossus;* the more medial muscle should have its origin on the hyals and is the *hyoglossus.* His *stylo-pharyngeus* and *superior constrictor* are not readily identifiable.

More complete accounts have been published of some of the other odontocetes. For the Phocoenidae, Boenninghaus' account (1902) of the throat of *Phocoena* deals in careful detail with the same region we have studied, and goes considerably further than we have in discussing development and homology. The lack of agreement of some of his plates with our dissections of delphinids led us to check his findings on an adult *Phocoena.* The discrepancies were mostly in the pharyngeal region and have been analyzed earlier. Briefly, it may be said that, where differences occurred, the arrangement of these muscles in *Phocoena* was more like that in the delphinids than like Boenninghaus' plates. Subsequent to Boenninghaus' work but without commenting on it, A. B. Howell (1927) described the myology of the neck and throat, exclusive of the pharynx, of *Neomeris,* another phocoenid. For this reason a synonymy of his musculature has been included.

The most recent comprehensive studies of this region in the Physeteridae are those of *Kogia* by Schulte and Smith (1918) on the muscles of the neck and throat, and by Kernan and Schulte (1918) on the muscles of the pharynx. Both of these studies have already been related to our work. Since these workers themselves have amply commented on the findings of earlier investigators, we have not repeated their comparisons.

For the Monodontidae, Hein's account (1914) of *Monodon monoceros* is the most pertinent. Though it is primarily of the larynx, it includes detailed descriptions of the interramal, tongue, and hyoideal muscles, and a synonymy of his names has been incuded in our text. His observations on the pharyngeal region, incomplete as they are because the hyolaryngeal complex had been cut away from the skull, suggest an arrangement very similar to that found by us. Watson and Young's earlier paper (1880) on *Delphinapterus leucas* includes the same interramal, tongue, and hyoideal muscles that we found, with the exception of the *mylohyoid, occipitohyoid,* and *hyoepiglotticus.* Of these, what they identify as *mylohyoid* is our *digastric,* while the other two as well as our *mylohyoid* are lacking. Howell (1930) described the interramal and throat musculature of *Monodon* as resembling that of *Neomeris* and uses the same names for muscles in both papers.

A recent rather hasty examination of *Ziphius* (Ziphiidae) suggests to us that it, too, is much the same.

The intranarial larynx, and its associated structures, seems to be such a successful adaptation for aquatic life that, once arrived at, it has varied little. Presumably this was a modification that occurred early in this adaptation. The arrangement of the structures involved is so peculiar and so different from that in land mammals that it seems unlikely to have been developed repeatedly. Those familiar with cetaceans will know that the families involved differ so widely in skull and external characters that the similarity in the myology of this region is all the more remarkable.

NOTE ADDED IN PRESS

In support of his theory that "during feeding and swallowing the larynx is freed, laid in the bottom of the pharynx and food passed over it" (in "Animals in aquatic environments: adaptations of mammals to the ocean," Chap. 46, Handbook of Physiology — Environment, Amer. Physiol. Soc., p. 744, 1964), Dr. John C. Lilly (personal communication 9 October 1964) reports of *Tursiops* that after he has forcibly disengaged the larynx by hand, the animal re-engages it without assistance.

While this observation is good evidence of the effectiveness of the muscles drawing the larynx into the back of the bony nares, it does not also show that the animal itself can voluntarily disengage the larynx. It does suggest that much of the time the muscles lifting the larynx are more important than the sphincter muscles in holding it in place. This is as would be expected, because contraction of the sphincter muscles holds the tip of the larynx shut, and during breathing and probably during phonation it needs to be open. In swallowing, however, the sphincter muscle would seem to be the more important, for contraction of this around the tip of the epiglottis would seal off the nares from the food passage, which here is directed somewhat dorsally as well as posteriorly, and so passes diagonally across the entrance to the bony nares. The atypical position of the passage, more posterior than ventral to the nares, and the absence of a soft palate, make some such arrangement for keeping the food out of the nose essential.

Dr. Lilly also writes (*ibid.*), "there is not room between the larynx and the bone of the lower jaw to pass food of the size which these animals normally swallow. . . . during feeding, one can palpate the throat region and find the larynx being pulled downward and pressed outwards during the swallowing act."

Actually the larynx lies posteroventral to the jaw (see Figs. 4 and 10) so there is no constriction of the passage between jaw and larynx. Probably what was felt were the ceratohyals which lie anterior to the larynx and near the external surface. Because of their close connection with the rest of the hyoid apparatus to which the tongue muscles are attached, movement of these during swallowing is to be expected. Posteriorly the larynx itself lies deep in the neck, internal to the thick sternohyoid.

That the larynx could not be "laid in the bottom of the pharynx" is clear also because the interrelations of aryteno-epiglottids, thyroid, and pharynx make the postulated action an impossibility. The thyroid and aryteno-epiglottid cartilages are firmly attached to each other (see Fig. 17) so that if they are moved ventrally they move as a unit. Further, since the pharynx itself is enclosed on each side between the thyroid and aryteno-epiglottids (Figs. 10, 11), and posterior to this the *thyreo-pharyngeus* wraps around the pharynx (Figs. 5-7, 9, 16), if the thyroid moves ventrally, it takes the pharynx with it. Dr. Lilly's observations would seem to show that internal pressure in the food passage may push the whole larynx ventrally unless this pressure is counteracted by the *occipitothyroid* muscle. Moving the larynx ventrally in this manner would not pronate the aryteno-epiglottids. It is not a muscular action and would be involuntary as far as the porpoise is concerned.

Aside from the anatomy involved, it seems unlikely that the intranarial larynx, an arrangement of such patent utility to an air-breather eating under water, would be undone and by-passed just when it is most needed.

EXPLANATION OF FIGURES

The drawings are all of actual dissections of single individuals, except for Figures 8 and 9. That part of the skull shown by broken lines was not drawn from the dissection but added later for purposes of orientation. Figures 1-7 are of progressively deeper dissections of a specimen of *Delphinus delphis.* Figures 8 and 9 are diagrammatic in that they are based primarily on a dissection of *Lagenorhynchus albirostris,* but have certain details added from a subsequent dissection of *L. acutus.* Figures 10 and 11, of the laryngeo-pharyngeal region, are photographs of *Stenella styx,* but are characteristic of all the Delphinidae. The rest of the figures are all of *Globicephala melaena.* Figures 12-15 are of progressively deeper dissections of a single individual; Figures 16 and 17 are of two other individuals.

ABBREVIATIONS USED IN THE FIGURES

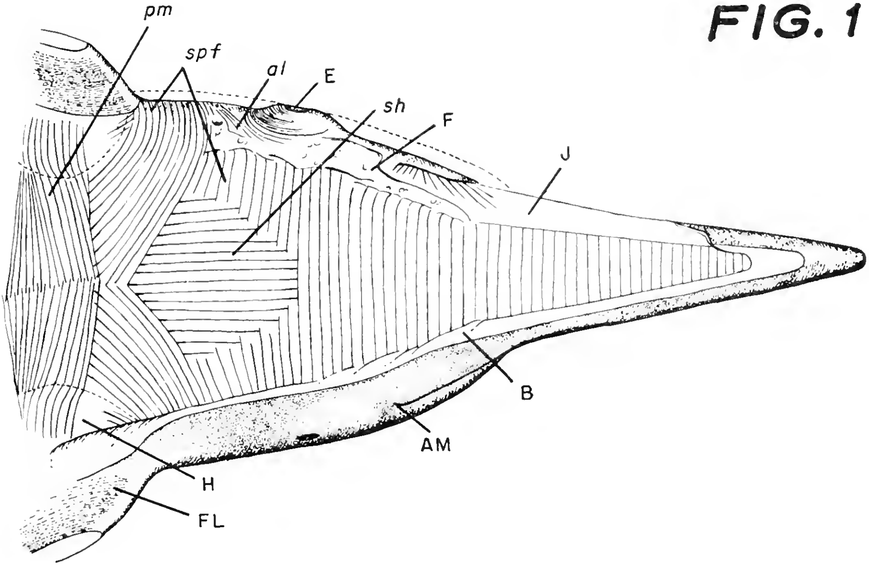
MUSCLES

al	*auriculolabialis*	*or*	*orbicularis oris*
ca	*cricoarytenoid*	*ot*	*occipitothyroid*
clo	*circular layer* of oesophagus	*pg*	*palatoglossus*
ct	*cricothyroid*	*pm*	*pectoralis major*
d	*digastric*	*pp*	*palatopharyngeus*
gg	*genioglossus*	*ppt*	*palatopharyngeus, pars thyropalatinus*
gh	*geniohyoid*	*ptp*	*pterygopharyngeus*
h	*hyoglossus*	*sc*	*scalenus*
he	*hyoepiglotticus*	*sg*	*styloglossus*
hl	*hyoglossus* lateral portion	*sh*	*sternohyoid*
hm	*hyoglossus* medial portion	*sm*	*sternomastoid*
ih	*interhyoid*	*sp*	*stylopharyngeus*
mh	*mastohumeralis*	*spf*	*sphincter colli profundus*
mps	*masseter, pars superficialis*	*spt*	*sphincter colli primitivus*
my	*mylohyoid*	*st*	*sternothyroid*
oc	*orbicularis oculi*	*t*	*temporalis*
oh	*occipitohyoid*	*th*	*thyrohyoid*
		tp	*thyreopharyngeus*

STRUCTURES OTHER THAN MUSCLES

A	arytenoid cartilage
AC	auricular cartilage
AM	angle of mouth
B	blubber
BC	buccal cavity
BH	basihyal bone
BU	bulla
C	cricoid cartilage
CH	ceratohyal cartilage
CJ	condyle of jaw
CO	occipital condyle
E	eye
EP	epiglottid cartilage
F	fat
FL	flipper
H	humerus
J	jaw (in each instance, right)
M	meatal tube and investing fibrous tissue
ML	melon
NP	nasopharynx
O	oesophagus
OP	oropharynx
P	pharynx
PA	palatine aponeurosis
PTL	pterygoid ligament
R	raphe
S	sternum
SH	stylohyal bone
T	thyroid cartilage
TH	thyrohyal bone
TO	tongue
TPH	tympanohyal cartilage
TR	trachea
W	see explanation, Fig. 10
X	see explanation, Fig. 10
Y	see explanation, Fig. 10
Z	zygomatic arch
ZP	zygomatic process of squamosal bone

FIG. 1



Delphinus delphis

Figure 1. Ventral view of gular region with blubber cut away to show superficial layer of muscles.

Delphinus delphis

Figure 2. Ventrolateral view with *sphincter colli profundus* and most of the *pectoralis major* cut away. Of the *sphincter colli primitivus,* only the part associated with the ear is shown; the small ear muscle posterior to this was not identified.

Figure 3. Ventrolateral view of interramal and tongue muscles. The *mylohyoid* has been entirely removed. The *geniohyoid* and *digastric* have been folded back at their insertions to show the underlying layers.

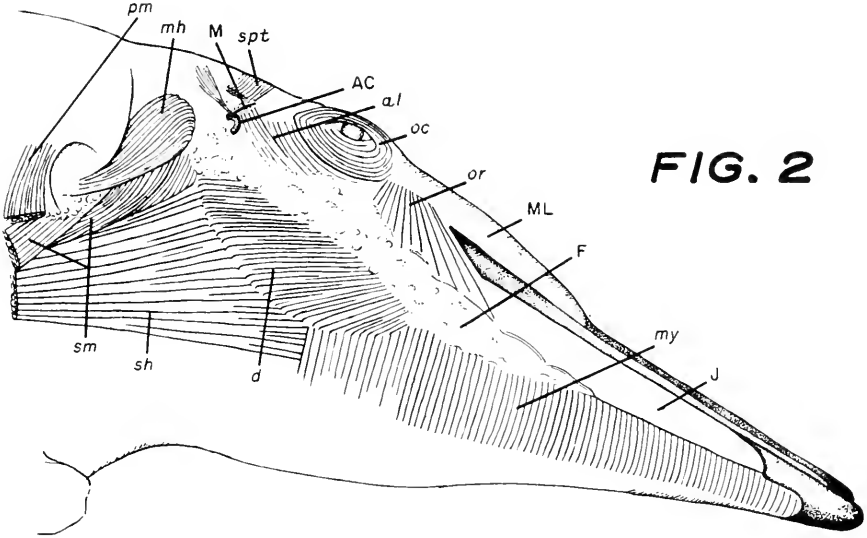

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FIG. 2

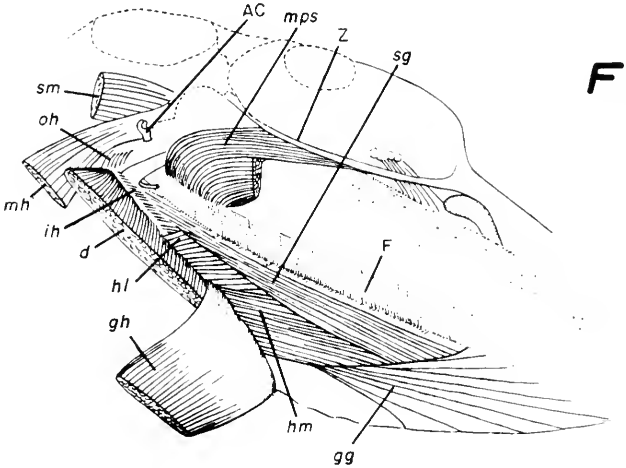
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FIG. 3

Delphinus delphis

Figure 4. Ventrolateral view of the hyoideal muscles. The *occipitohyoid* has been cut away, causing the tip of the thyrohyal to sag ventrally. The origins of the *hyoglossus, styloglossus* and *genioglossus* have also been removed.

Figure 5. Same view as Figure 4. The thyrohyal bone and the external muscle layers have been removed to show the deeper layers of the hyolaryngeal region, and the hyoid cartilages have been drawn away from the base of the skull. The pharynx has been dissected away from the bony palate, and pharynx and tongue folded down as a single mass. The zygomatic process of the temporal bone, and the frontal bone dorsal to the orbit, have been partly removed.

FIG. 4

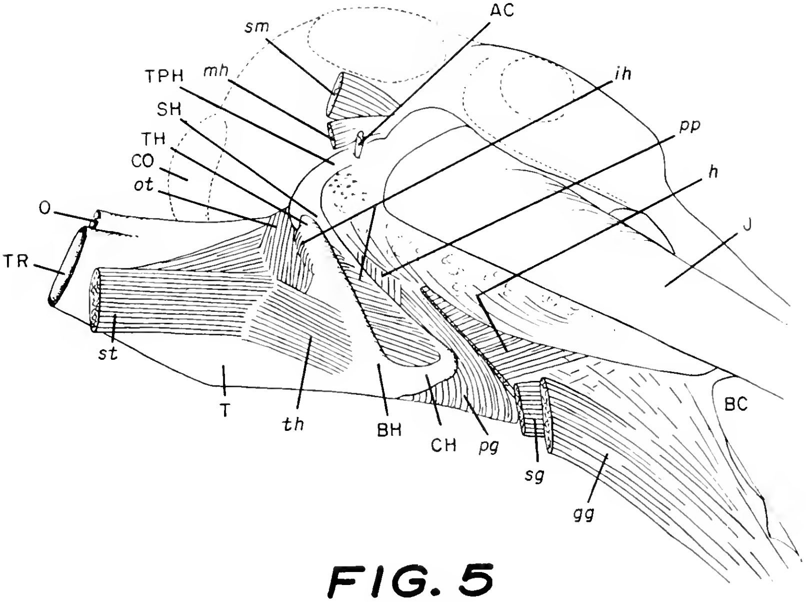
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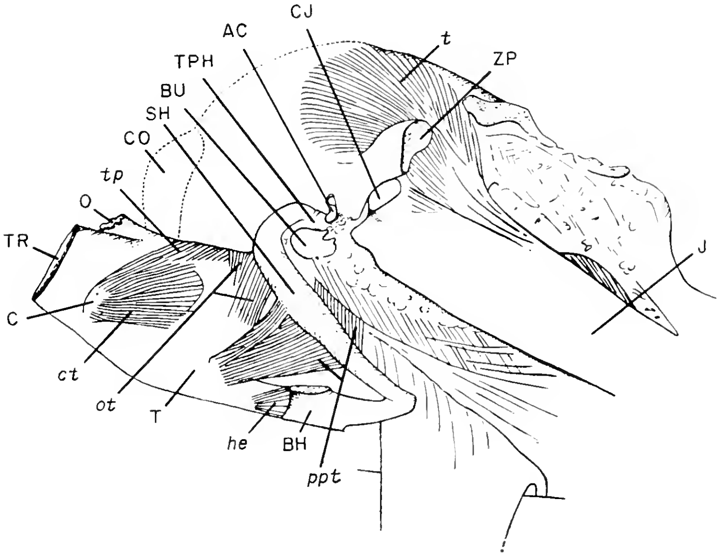
FIG. 5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Delphinus delphis

Figure 6. Same view as Figure 4. The tympanohyal has been cut away from the occipital posterior to the bulla, and the stylohyal pulled ventrally and rotated outward to show the *stylopharyngeus* going into the posterior bony nares, as well as the attachments of the *palatopharyngeus.* Part of the jaw has also been removed. The right side of the pharynx is shown passing lateral to the epiglottis.

Figure 7. Details of the *palatopharyngeus.* All of the hyals except part of the stylohyal have been removed. The cranial attachment of the *occipitothyroid* has been cut and the larynx has been pulled ventrally. In order to show the inner layers of the *palatopharyngeus* which surround the arytenoepiglottid cartilages, the *pars thyropalatinus* has been cut away from the pterygoid ligament and this whole outer part folded down. For the same reason the *stylopharyngeus* has been cut near its insertion and folded up. Part of the thyroid cartilage has also been removed to show the laryngeal attachments of the *pars thyropalatinus.* The main mass of the *palatopharyngeus* may be seen passing into the bony nares.

FIG. 6

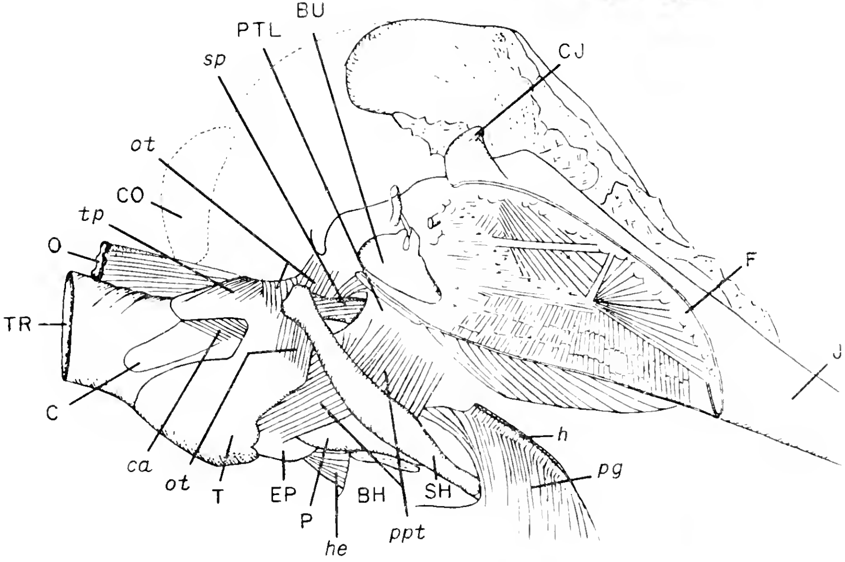
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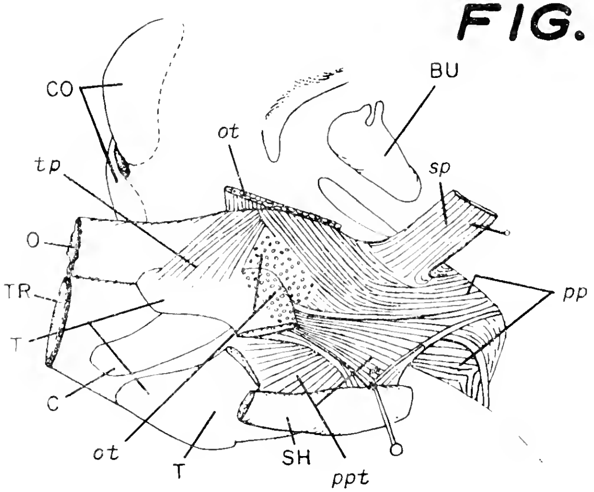
FIG. 7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Lagenorhynchus albirostris and *L. acutus*

Figure 8. Ventral view of hyoid apparatus and tongue muscles. The more superficial layers are on the lower half of the figure; the area of insertion of the *mylohyoid* is shown on this side only and, on this side, the origin of the *hyoglossus* has been cut away entirely to show the underlying *interhyoid*. In the upper half of the figure the deeper layers are shown; parts of the *stylo-* and *hyoglossus* have been removed and both muscles folded outward to show their relation to *palato-* and *genioglossus* at their insertion in the tongue.

Figure 9. Nasopharynx and the entire laryngeo-pharyngeal region, including bones and cartilages, cut away from the skull. The relation of *stylo-*, *palato-*, and *pterygopharyngeus* at their insertion in the walls of the nasopharynx is shown here. The approximate outline of the larynx within the nasopharynx is indicated by broken lines. The approximate boundary internally between palato- and pterygopharyngeus is shown by the straight broken line.

FIG. 8

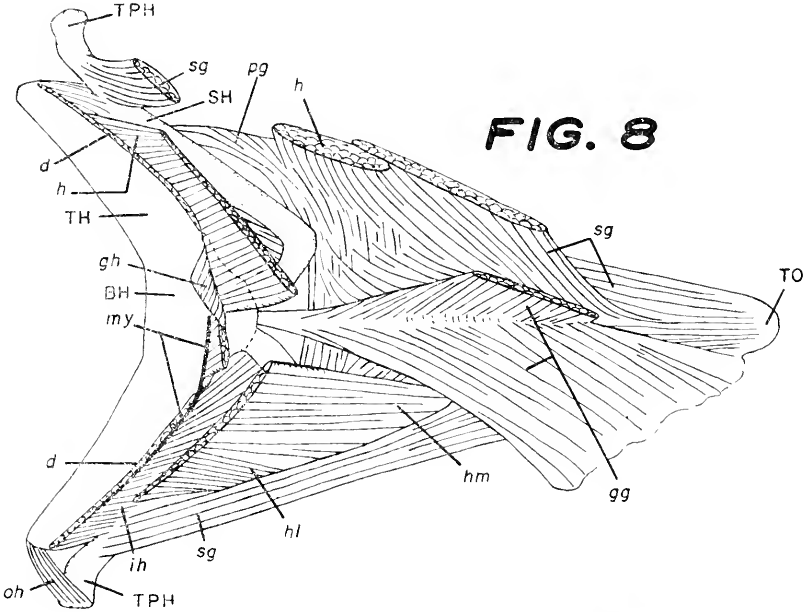
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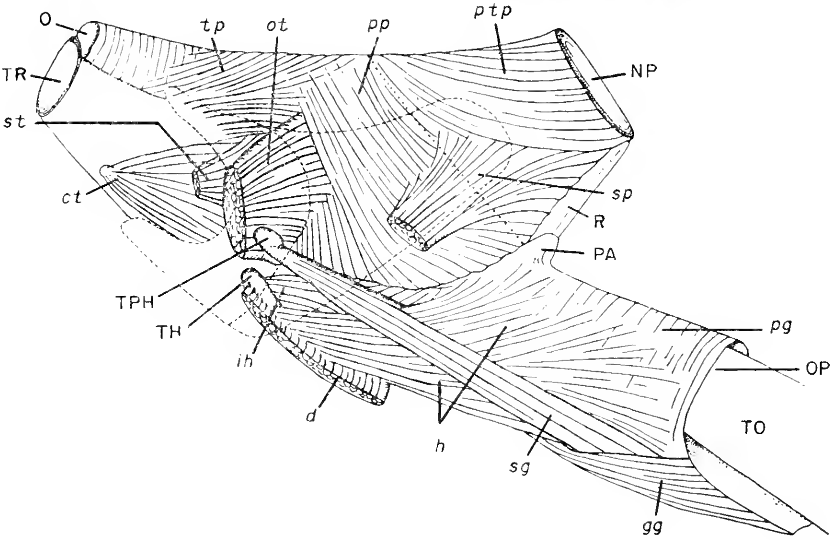
FIG. 9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Stenella styx

Figure 10. Photograph of dissection showing intranarial position of larynx. The right thyrohyal and stylohyal bones, the wing of the thyroid, and part of the pharyngeal musculature have been removed, and the passage from the buccal cavity to the oesophagus laid open by a longitudinal slit through the right wall. The probe lies in the left side of the divided passage, the right side having been cut open. Dorsal to it, the cut ends of the pharyngeal musculature show at X. The tooth rows at Y are those of the left side. The posteroventral slope of the bony palate shows well in this picture; it ends at W, posterior to which lies the short palatine aponeurosis.

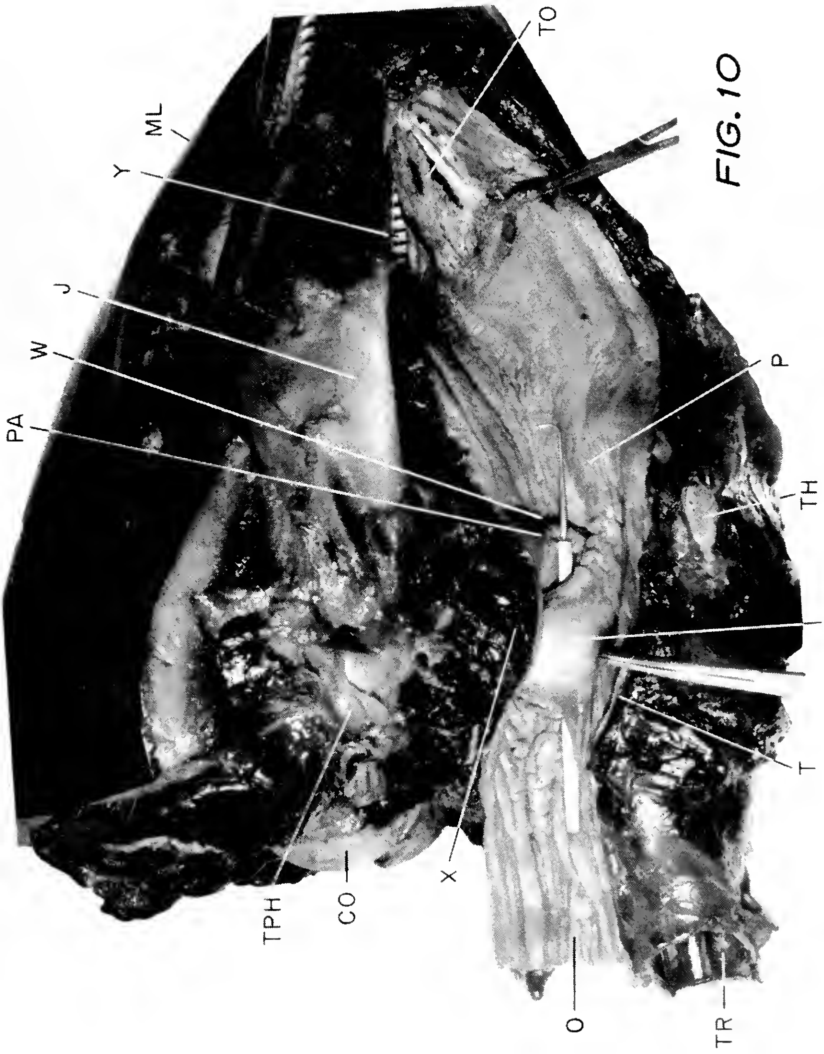

FIG. 10

Stenella styx

Figure 11. The same dissection as Figure 10 with the larynx withdrawn to show its height in relation to the diameter of the passage.

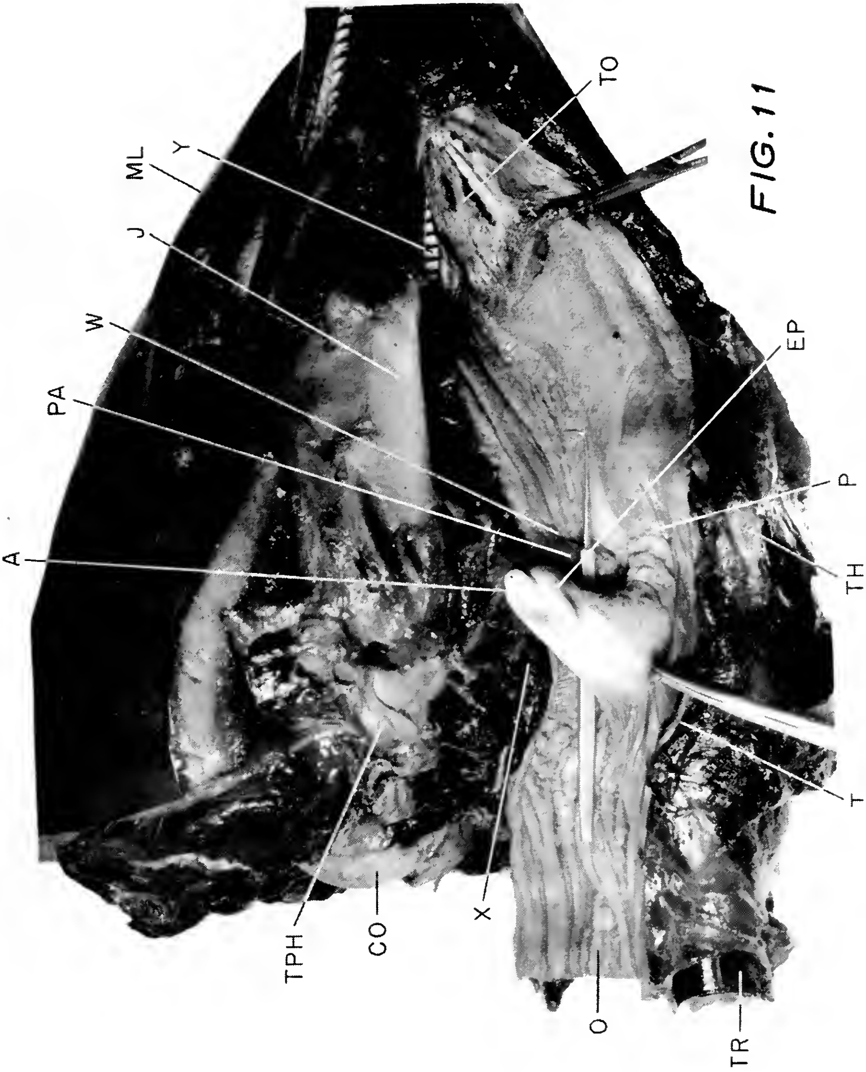

FIG. 11

GLOBICEPHALA MELAENA

Ninety years have gone by since Murie published his excellent and remarkably detailed morphology of *Globicephala melaena* based on a single specimen considerably advanced in decay. Since then few workers have had the patience or the opportunity to re-examine his findings, so Murie's work has remained the standard for students of odontocete structure. A recent unsuccessful attempt to apply his descriptions to the myology of the throat and tongue in certain related delphinid genera has led us to an examination of this region in *Globicephala melaena*. This has brought to light certain discrepancies in Murie's work between text and figures, as well as between his figures and actual specimens. Some of these are misleading to a student of function, and the present attempt is to clarify, not derogate from Murie's classic. In general, our findings are substantially as stated in his text, though sometimes a little more detailed. Such errors as we have found have been largely in his plates. Some discussion is included of Macalister's work on *Globicephala* (1867), to which Murie often refers.

In making this comparison, four fresh-killed individuals were dissected, each in a slightly different way, a special effort being made to duplicate the various aspects figured by Murie. This has shown that some of his figures must have been based on a reconstruction or interpretation of what he found, not on the actual dissection, and it is in such figures, particularly numbers 11 and 12 on his plate 31, that the majority of errors occur. For purposes of orientation, we figure a few adjacent muscles of the neck and upper thoracic region, but details of their attachments have not been worked out.

MUSCLES OF THE NECK AND THROAT

Sternomastoid muscle (Fig. 12, *sm*). The *sternomastoid* is as described by Murie (p. 282). Its origin on the mastoid is internal and slightly ventral to the *mastohumeralis*, its insertion on the sternum is superficial and posterior to the *sternohyoid*.

Mastohumeralis muscle (Fig. 12, *mh*). The *mastohumeralis* (*cephalo-humeral* of Murie, p. 274) is essentially as he describes it. Its origin on the mastoid is external and dorsal to that of the *sternomastoid* and its insertion is on the anterior part of the head of the humerus.

Scalenus muscle (Figs. 13-15, *sc*). The relation between Murie's *obliquus* muscles and his *scalenus* is not entirely clear.

His *scalenus* (fig. 68) appears to attach medially on the exoccipital, and subsequent authors (Schulte and Smith [*Kogia*], 1918, fig. 16, p. 49; Howell [*Neomeris*], 1927, fig. 3, p. 9) have called the large muscle attaching in this area *scalenus*. We ourselves, having made no dissection of the neck muscles, have followed these authors, whose identification of *scalenus* is confirmed by Fraser and Purves (*in litt.*).

Mylohyoid muscle (Fig. 12, *my*). The *mylohyoid* (Murie, *mylo-hyoid,* p. 251) is a rather thin sheet of transverse fibers, coarse in structure, and extending from the symphysis of the jaws to the thyrobasihyal region. Anteriorly, it attaches on each side between the mandible and the tongue; posteriorly, it passes between the *digastric* and *geniohyoid* to end in the fatty mass internal to the jaw. Here the muscle itself becomes very fat and merges with the insertion of the *digastric.*

The apparent origin of the *mylohyoid* in Murie's figure 11 is misleading, as it seems to arise jointly with the *sterno-hyoid* from the thyrohyal cartilage. Actually its connection with the thyrohyal is internal to the *digastric*, where the fasciae of both muscles merge.

Digastric muscle (Fig. 12, *d*). The muscle which we have called the *digastric* appears to be that which Murie tentatively identifies thus (p. 251), even though he describes (p. 252) and figures (fig. 63) it rather differently. It takes origin broadly from the thyrohyal cartilage and in part also from the strong fascia which runs from the tip of the thyrohyal to the cranial attachment of the tympanohyal cartilage. This is a fat muscle, becoming increasingly so towards its insertion in the fatty mass along the margin and outer surface of the posterior part of the jaw.

Murie does not include the *digastric* in his figure 58, but his *styloglossus* [*sic*] of this and of figure 11 apparently takes origin from the thyrohyal cartilage and bears the same relation to his *genio-hyoid* and *sterno-hyoid* as does our *digastric*. His *styloglossus* differs from our *digastric* only in being inserted too near the symphysis of the jaw. Probably, then, this and the *digastric* of page 251 and figure 63 are the same, as well as being that which we have called *digastric.*

Geniohyoid muscle (Fig. 12, *gh*). The apparently single *geniohyoid* arises via fascia from the anterior part of the ventral surface of the basihyal cartilage, where it is partially covered by the *sternohyoid.* Thence it passes anteriorly to the mandibular symphysis. Murie describes (p. 252) and figures (fig. 11) paired *genio-hyoidei* which otherwise resemble ours.

M. styloglossus (Figs. 13, 14, 16, *sg*). The *styloglossus* takes origin rather narrowly from the anterior and ventral margin of the midsection of the stylohyal cartilage. It passes forward beneath the *digastric*, widening as it goes, to insert in the side of the tongue, external to the *hyoglossus* and internal to the *genioglossus*. Murie (p. 252) describes a muscle which he tentatively identifies as the *stylo-glossus* [*sic*] as taking origin from "nearly all the anteroinferior edge of the stylohal," but since he supposes this muscle to be external to the *hyoglossus* which takes origin broadly on the thyro- and basihyal cartilage, such a broad origin for the *styloglossus* is not possible. On the other hand, his description of the outer head of the *hyo-glossus* (p. 252) matches closely our *styloglossus*. The discrepancy is one of muscle names, not numbers of layers, for, while Murie's text indicates that there are three distinct sections of muscle, two parts of a *hyoglossus* and a single *stylo-glossus*, in a region where we only found two, the left hand side of his figure 11 (right side of dissection) shows no more layers than we found. In this figure, the thyrobasihyal complex is too broad, with a consequent distortion in the position of the origin of various tongue muscles relative to each other. If one makes allowance for this and for the difficulty of determining the actual fiber direction of certain of the muscles, the figure resembles fairly closely the situation we found, Hg^1 being our *styloglossus*, Hg^2 our *hyoglossus*, while the muscle he labels Stg is our *digastric*. In his figure 6, Sg is apparently the same as our *styloglossus*.

M. hyoglossus (Fig. 13, *h*). The *hyoglossus* takes origin broadly along the anterior edge of the thyro- and basihyal cartilages internal to the *digastric* and *geniohyoid*, with a few fibers from the junction of the basi- and ceratohyal cartilages. It inserts in the side of the tongue internal to the *styloglossus*. This is substantially as described by Murie (*hyo-glossus* p. 252), although it does not appear to be two-headed and has no stylohyal attachment. It is the muscle labeled as Hg^2 in his figure 11.

M. genioglossus (Fig. 13, *gg*). The *genioglossus* on each side passes upwards, forwards, and outwards from the inferior median raphe to insert anteriorly in the tissue lining the buccal cavity. Posteriorly its origin is in the root of the tongue internal to the hyal cartilages, rather than from the hyals themselves. This is the muscle called *genio-hyoglossus* by Murie (p. 252), and agrees well with his description except for the absence of hyal attachments.

M. palatoglossus (Fig. 16, *pg*). This muscle is much as described by Murie (*palato-glossi*, p. 254), though we found it not quite so thick. The transverse fibers lining the roof of the mouth are closely bound to the bony palate and at their insertion mingle chiefly with the *hyoglossus*.

Sternohyoid muscle (Fig. 12, *sh*). The *sternohyoid* (Murie, *sterno-hyoidei*, p. 263) is a thick, strong muscle arising on the sternum as well as the first costal cartilage, and inserting broadly on the thyro- and basihyal cartilages posterior to the *digastric*. Medially, its fascia partially covers the insertion of the *geniohyoid*.

In Murie's figures 58 and 63, the muscle labeled *sterno-thyroid* is too superficial for this and agrees well with our dissection of the *sternohyoid*, which it probably is. No such confusion exists in his figure 11, where the *sternohyoid* is the more superficial of the two.

Sternothyroid muscle (Figs. 13, 17, *st*). The *sternothyroid* on each side is indistinctly divided into two parts which merge completely at their sternocostal origin. The more dorsal, which is the thicker part, takes origin on the anterior margin of the first rib. The more ventral, more sheetlike portion takes origin slightly internal to the anterior border of the sternum. Both insert on the thyroid cartilage with a very thin slip extending on top of the thyrohyoid. Murie's description (p. 263) of the *sterno-thyroidei* matches our dissections well, while his figure 11 shows the rather narrow appearance of this muscle when seen from the ventral aspect.

Thyrohyoid muscle (Figs. 13, 14, 15, 17, *th*). The paired *thyrohyoid* muscles lie internal to the *sternohyoid* and are essentially as described by Murie (*thyro-hyoidei*, p. 263). This is the same muscle which he figures under a different name — *thyroideus* — in figure 11.

Occipitohyoid muscle (Figs. 12, 13, 14, *oh*). The *occipitohyoid* is a superficial muscle which takes origin in the tissue near the articulation of the stylohyal with the skull. It passes across this cartilage to insert on the lateral tip of the thyrohyal. Murie describes no such muscle, but refers (p. 264) to a muscle which takes origin near the auditory canal and inserts halfway down the stylohyal; presumably this is the muscle called *squamostyloid* in his figure 13. The muscle as figured by him is unlike any muscle we found, nor does his figure match Macalister's description of the *stylo-keratic* (1867, p. 480) or Carte and Macalister's of the *squamostyloid* (1868, p. 235), with both of which Murie homologizes the unnamed muscle described on page 264. The situation is further confused because both Macalister and Murie give a stylohyal insertion for their muscle. Our dissections show a single muscle in this region, which differs from Murie's and Macalister's descriptions in its thyrohyal rather than stylohyal insertion. Material in poor condition could easily give rise to such an error, and so it can be assumed that our *occipitohyoid* is not only the same as the *occipitohyoid* of Rapp (1837, p. 132) and Stannius (1849, p. 7), which it matches closely and with which Murie also homologizes his muscle, but also equivalent to the above-mentioned *stylo-keratic* and *squamostyloid.*

Interhyoid muscle (Figs. 13, 14, *ih*). The *interhyoid,* as described and figured by Murie (*interhyoideus,* p. 264 and figs. 11 and 13), fills the space between the combined stylo- and ceratohyal cartilages and the thyrohyal cartilage. It is undoubtedly homologous, as he says, with Macalister's *hyo-keratic* (1867, p. 480).

MUSCLES OF THE PHARYNX

This is a difficult region to understand, even when series of freshly killed specimens are available for dissection. Murie had only one far-from-fresh specimen, and so it is not surprising that his descriptions of the muscles in this region are rather sketchy, and that there are certain discrepancies between his text and plates. Neither fit entirely with our findings. We have found it equally difficult to apply all of Macalister's description to the various muscles found by us. The situation is further complicated by these authors' use of many of the same muscle names, but not always for the same muscles, and by their attempts to identify standard mammalian muscles in this very non-standard mammal. For this reason it seems best to redescribe the pharyngeal-postnarial region; Murie's comments will be discussed in the light of our findings, not ours as supplementary to his. The arrangement of muscles is remarkably similar to that found in the delphinids, and the names we use are those of section one of this paper.

No *levator* and *tensor palati* as described by Murie (p. 255) were found, and the muscle identified as Lp in figure 30, which is of *Lagenorhynchus albirostris,* is probably different from the *levator palati* discussed in the text. The muscle which we found attaching posterolateral to the fibrous mass around the bulla, as the figure of Lp appears to show, is the *occipitohyoid.* Murie's Lp as figured is too large for this, and there is no indication of a thyrohyal attachment. Possibly this Lp is the *stylopharyngeus,* but most probably it is, in reality, one of the neck muscles, perhaps *scalenus.* The text states that "the levator muscle covers the interspace of the pterygoid plates and the Eustachian enlargement; it is fleshy forwards on the palate, narrows posteriorly, and is fixed fibrotendinously near the tympanic region." This is the region where the *palatopharyngeus, pterygopharyngeus,* and *stylopharyngeus* are found, and no part of these matches this description. In other words, with the muscle only partially figured and incompletely described, it seems best not to identify it with any of the known muscles of the region. The same is true of the *tensor palati,* which is said to be closely associated with the *levator.*

M. stylopharyngeus (Fig. 16, *sp*). The *stylopharyngeus* arises rather narrowly from the dorsomedial surface of the stylohyal cartilage, where it is difficult to separate from the *palatopharyngeus.* It widens as it passes anterodorsally across the *palatopharyngeus* to merge with the *pterygopharyngeus* at its insertion in the walls of the nasopharynx. This is clearly the same as Murie's *stylo-pharyngeus* (p. 255, and fig. 12). In this same figure Murie shows on the opposite side a *stylohyoideus* in much the same relative position as the *stylopharyngeus,* though he does not describe this in the text. However, he does (p. 264) quote Stannius as describing a *stylohyoid* in *Phocoena.* Murie feels that this is equivalent to his *interhyoideus.* This latter is quite a different muscle from the *stylopharyngeus,* and is one which we also have found. The dorsal dissection of the pharyngeo-laryngeal region which Murie attempted to show in his figure 12 is difficult to make and interpret, and the actual relationship of the different layers is rather different from that figured. Between the stylohyal and the pharynx we found only one muscle, the *stylopharyngeus,* Murie's *stylohyoideus* on the other side being very likely a mislabeling of the same.

M. palatopharyngeus (Fig. 16, *pp*). The *palatopharyngeus* takes origin from the pterygoid ligament across the palatine aponeurosis and into the bony nares. Here, anteromedially, it merges so completely with the *pterygopharyngeus* that the exact origin of each could not be determined. From its origin, part of the muscle passes posteroventrally to attach along the stylohyal cartilage, and part of it sweeps back around the nasopharynx, passing ventral to the *stylopharyngeus* which is closely bound to it, to insert in the posterior wall of the nasopharynx. Here again its fibers merge with those of the *pterygopharyngeus*, and are also partly overlaid by those of the *thyreopharyngeus*. Another portion of the *palatopharyngeus* goes from the stylohyal cartilage to insert on the internal surface of the thyroid cartilage. This portion is not shown in the accompanying figures, but in a lateral dissection of the hyo-laryngeal region after the *thyrohyoid* and the thyrohyal bone are cut away, it shows as a conspicuous mass passing from the inner surface of the thyroid to the stylohyal bone. In general, this muscle matches the more ventral part of Murie's *constrictor superior*. Murie does not describe this muscle, but figures it (fig. 12) anterior to the stylohyal bone; this must be an error, as we found no muscle here between the *styloglossus* and *palatoglossus*. In addition to identifying the very complex mass of *pterygo-* and *palatopharyngeus* as a single muscle, the *constrictor superior*, Murie also mentions (p. 254) a *palatopharyngeus*, referring to Macalister's account. Macalister's description (p. 480), except for omitting the stylohyal attachments, matches our *palatopharyngeus* quite well.

M. pterygopharyngeus (Fig. 16, *ptp*). The *pterygopharyngeus* is a powerful muscle which passes down the bony nares to merge with the *palatopharyngeus* and wrap around the tip of the arytenoepiglottid cartilages in a strong sphincter. It is intimately connected with the *stylopharyngeus* also, and takes origin on the walls of the bony nares anteriorly; the fibers are at first longitudinal and then, as described by Murie (p. 254), "assume an oblique and spiral direction" to surround the tip of the larynx, and insert in the posterior wall of the nasopharynx chiefly anterior to the insertion of the *thyreopharyngeus*, though a few fibers mingle with this latter. This is that part of Murie's *superior constrictor* which has no thyroid attachment and is shown in his figure 12 as Cs.

Occipitothyroid muscle (Figs. 13-17, *ot*). Two partially separate sections are recognizable, an outer which takes origin on the stylohyal bone near its cranial attachment and on the basioccipital medial to the stylohyal, and an inner, larger portion which takes origin on the basioccipital anterior to the *scalenus*. Together they insert on the anterior and upper portion of the outer surface of the horn of the thyroid cartilage.

The inner part inserts also more posteriorly on the medial surface of the horn of the thyroid as well as on the pharynx, where its fibers mingle with those of the *thyreo-* and *pterygopharyngeus.* The *occipitothyroideus* of Murie's text (p. 265) is clearly the same as our *occipitothyroid*, although we failed to find the thyrohyal attachment mentioned by him. In our specimens the muscle passed beneath the tip of the thyrohyal bone without attaching to it. The muscle labeled *occipitothyroid* in Murie's figure 11 is misleadingly small. Adjacent to this, and not labeled, is a larger muscle, apparently with stylohyal attachments. The relation of the bones and cartilages as shown here is not quite as we found them, but allowing for a certain error, this muscle could either be the external part of the *occipitothyroid* or, if the stylohyal attachment is correct, the *palatopharyngeus.* Murie's dorsal view of this region shows no cranial attachments for any of the muscles here. This is clearly an error, but, from the position relative to the adjacent layers of the muscle labeled *constrictor medius*, we incline to believe that it is the inner layer of our *occipitothyroid.* Murie's brief description of his *constrictor medius* could easily fit our *occipitothyroid.* Macalister's *stylopharyngeus* (p. 480) is the outer part of our *occipitothyroid*, and his *basio-thyro-hyoid* is the inner.

M. thyreopharyngeus (Figs. 14-17, *tp*). The *thyreopharyngeus* arises chiefly from the outer surface of the horn of the thyroid, with a few fibers from the inner side. It passes anterodorsally to insert on the pharynx. Posteriorly, at its insertion, it merges with the circular layer of the oesophagus, and anteriorly, it meets the *pterygopharyngeus* in an aponeurotic sheet. This matches Murie's description and figure (p. 254, and fig. 12) of the *inferior constrictor.* Referring to Stannius' description of *Phocoena*, he says (p. 255) that if a *thyreopharyngeus* exists in *Globicephala* it is probably part of "the constrictor."

CONCLUSION

The foregoing account is in no sense meant to replace Murie's work, nor is it intended to be a complete description of the region studied. Rather it has been the purpose of the authors to amend Murie's myology in order to make his general and excellent descriptions of the gross anatomy of the head and throat more useful to anatomists.

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Globicephala melaena

Figure 12. Ventrolateral view of head and neck with *sphincter colli* and associated layers removed; part of *mylohyoid* also cut away.

Figure 13. Same view, deeper dissection to show tongue muscles.

For abbreviations used in figures, see pp. 36-37.

FIG. 12

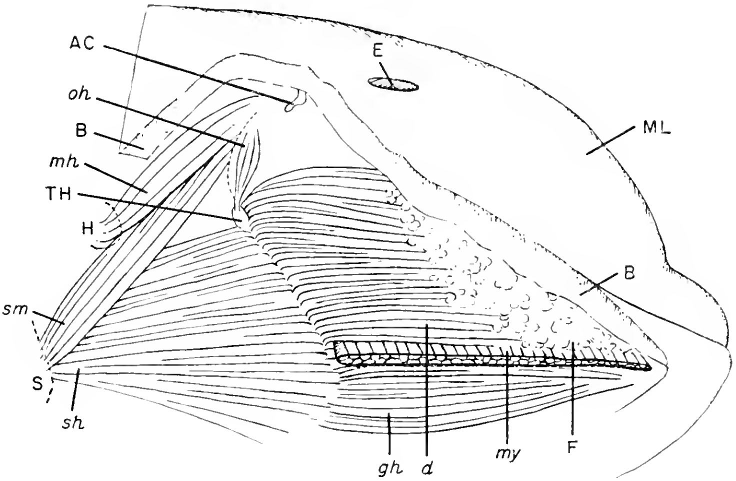
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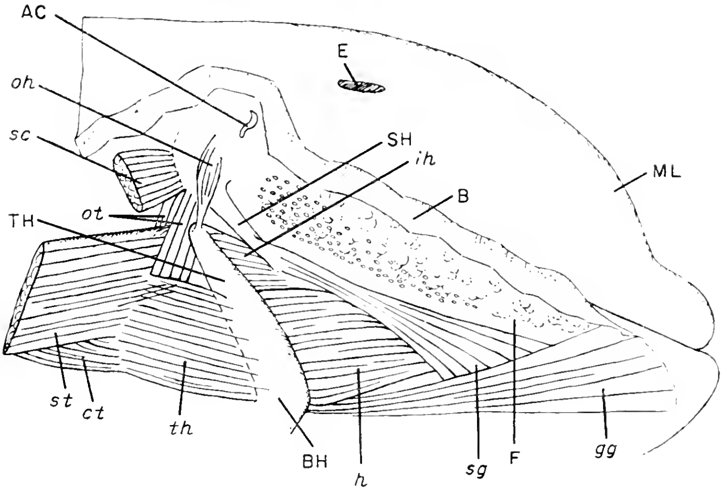
FIG. 13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Globicephala melaena

Figure 14. Tongue and sternal muscles cut away to show, in lateral aspect, the outermost of the muscles binding the hyolaryngeal apparatus together and to the base of the skull.

Figure 15. Dorsolateral view of same muscles.

For abbreviations used in figures, see pp. 36-37.

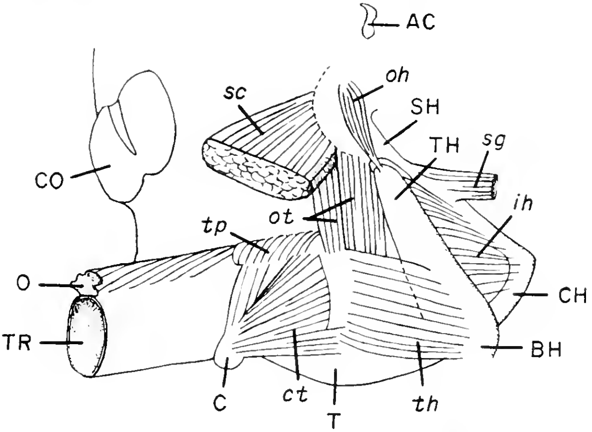
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FIG. 14

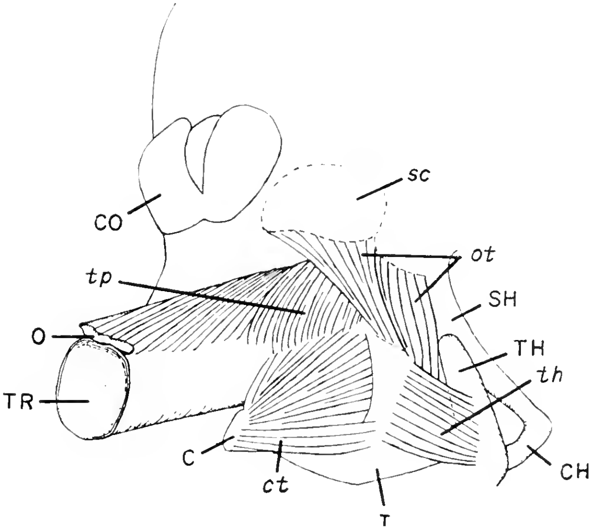
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FIG. 15

Globicephala melaena

Figure 16. Dorsal view of pharyngeal region detached from skull by dissecting the nasopharynx away from the bony nares and by cutting the tympanohyal cartilage and the *occipitothyroid* muscle. Anterior is to the right of the plate; this is the view figured by Murie (1873, pl. 31, fig. 12).

Figure 17. Lateral view of areas of muscle insertion on the larynx. This general arrangement is the same in all the odontocetes discussed.

For abbreviations used in figures, see pp. 36-37.

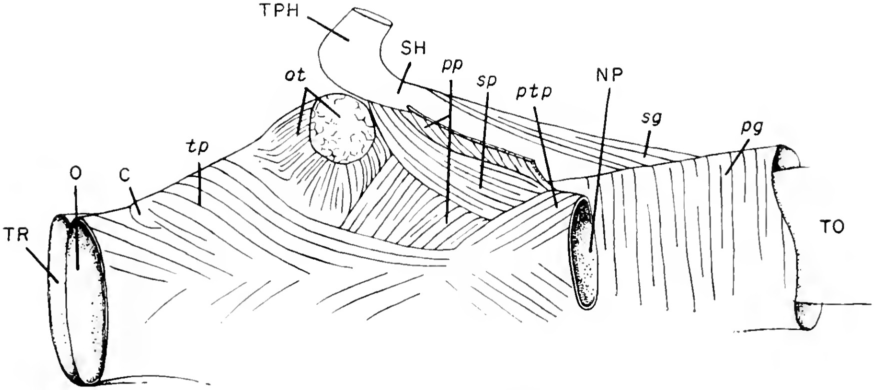

FIG. 16

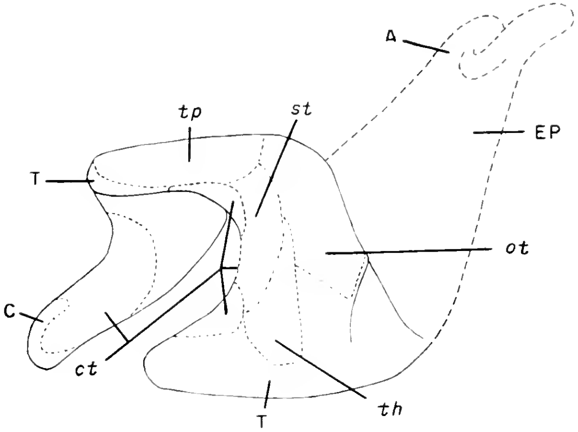

FIG. 17

Bulletin of the Museum of Comparative Zoology

HARVARD UNIVERSITY

Vol. 133, No. 2

A REVISION OF THE GENUS *RHABDEPYRIS* IN THE AMERICAS (HYMENOPTERA, BETHYLIDAE)

By Howard E. Evans

With Seven Plates

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
May 26, 1965

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Phylogeny and Evolution of Crustacea. Proceedings of a conference held at Cambridge, Mass., March 6-8, 1962. H. B. Whittington and W. D. I. Rolfe, editors. Cambridge, Mass., 192 pp., 80 figs., 1963. Cloth bound, $6.75.

Fishes of the Gulf of Maine, by Henry B. Bigelow and William C. Schroeder. Washington, viii - 577 pp., 1953. Photo-offset reprint, $6.50.

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The remaining stock of the scientific periodicals of the Boston Society of Natural History has been transferred to the Museum of Comparative Zoology for distribution. Prices for individual numbers may be had upon request.

Bulletin of the Museum of Comparative Zoology
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Bull. Mus. Comp. Zool., Harvard Univ., **133**(2):67-151, May, 1965

No. 2 — *A Revision of the Genus* Rhabdepyris *in the Americas (Hymenoptera, Bethylidae)*[1]

By Howard E. Evans

Rhabdepyris is possibly the most generalized of the several genera which comprise the bethylid tribe Epyrini, and within it may be seen trends in the directions of many of the other genera of this tribe. Thus, the hairy-eyed species (subgenus *Trichotepyris*) grade almost imperceptibly into *Anisepyris;* the small, smooth-eyed, hairy-bodied species (subgenus *Rhabdepyris*) differ from *Laelius* only in their more complete wing venation; and the larger, smooth-eyed, smooth-bodied species (subgenus *Chlorepyris*) closely approach *Epyris* and other genera with paired pits on the scutellum. It is important that the systematics of *Rhabdepyris* be well understood if progress is to be made with the remaining genera of this complex. I do not have enough material to treat the Old World fauna at this time, but I present here a preliminary review of the 41 known American species.

The generic diagnosis and key for separation from other Epyrini which I presented in 1964 (Bull. Mus. Comp. Zool., 132: 91-96) will suffice for present purposes. A review of the structure and terminology employed in this series of papers will also be found there, and the acknowledgments and sources of material listed there may also be taken to apply to the present paper. An alphabetical listing of the abbreviations used for body structures and for museums will be found at the conclusion of this paper. Also appended are a check list and an index of the American species.

Although in 1964 I placed *Trichotepyris* and *Chlorepyris* in the synonymy of *Rhabdepyris,* I now find it convenient to use these names for subgenera. The types of *Trichotepyris* and *Rhabdepyris, sensu stricto,* are Palaearctic species which I have not seen. It seems probable that our species are consubgeneric with the Palaearctic species, but I cannot be certain of this. Kieffer used the name *Chlorepyris* to apply to species with paired scutellar pits connected by a narrow groove, but as so defined *Chlorepyris* presents no real morphological gap from such species of *Rhabdepyris* as, for example, *origenus* Kieffer.

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[1] Supported by a grant from the National Science Foundation, GB-1544.

Chlorepyris is here redefined in a broader sense, to include all glabrous-eyed species in which the body setae are short, pale, and subappressed.

It is difficult to know which of the three subgenera should be regarded as most primitive; actually each is rather generalized but has at least one specialized feature. All of our species of *Rhabdepyris, sensu stricto*, are small and black, while both *Trichotepyris* and *Chlorepyris* show trends toward larger size, bright metallic colors, and blotching on the wings. In the latter subgenus one finds unusual modifications of body sculpture, including a tendency for the scutellar groove to be widened into pits on the sides and reduced to a thin line medially.

In all three subgenera the wing venation is much alike (see fig. 63 in Evans, 1964); I have therefore made no mention of venation in the keys and descriptions. The male genitalia are also relatively uniform in structure. They are not wholly without characters, but the differences seem to me too small to justify the difficulties in extracting and mounting these minute structures.

KEY TO SUBGENERA OF RHABDEPYRIS

1. Eyes covered with short setae; males with antennal segment three reduced to a small ring-joint closely consolidated with four (Fig. 18) .... B. TRICHOTEPYRIS Kieffer

   Eyes glabrous; males with antennal segment three of variable length, sometimes short and transverse but always well separated from fourth segment (Figs. 19-24, 71-73) 2

2. Body and major wing veins clothed with coarse, fuscous setae; pronotum short, its posterior margin paralleled by a foveolate groove; small, black species .... A. RHABDEPYRIS Kieffer

   Body and wing veins with only fine, pale setae; pronotum fairly long, its posterior margin not paralleled by a foveolate groove; small to moderately large species of black or metallic green or blue coloration .... C. CHLOREPYRIS Kieffer

A. Subgenus Rhabdepyris Kieffer

Rhabdepyris Kieffer, 1904, Bull. Soc. Hist. Nat. Metz, (2)11: 32 (type species: *R. myrmecophilus* Kieffer 1904; designated by Kieffer, 1906).

Subgeneric characters. — Small species of black coloration, without metallic reflections; eyes glabrous, but body and major wing veins clothed with rather large, subappressed to suberect black setae; scape and legs with shorter black setae; middle tibiae without spines. Mandibles small, in females with two sharp apical teeth and a series of three smaller teeth basad of these (sometimes indistinct), in males with five strong teeth; base of mandibles far removed from bottoms of eyes, the malar space greater than width of mandibles at their base; antennal scrobes not margined; males with third antennal segment much longer than second, nearly as long as fourth segment. Pronotum rather short, sloping strongly to the collar, its posterior margin paralleled by a foveolate groove; notauli often not reaching anterior margin of mesoscutum; scutellar groove strong; propodeal disc only slightly (1.1-1.3 x) wider than long, with five to nine discal carinae, transversely striate, the side-pieces never striate but more or less alutaceous or beaded. Mesopleurum rather irregularly ridged and pitted, the foveae not clearly formed, the lower fovea, when discernible, divided into two by a vertical or oblique ridge. Claws very weakly dentate, the tooth tending to slope outward.

Remarks. — I have not seen the type species, *myrmecophilus*, and consequently use *Rhabdepyris* as a subgeneric name rather tentatively for this complex. The six known American species have all remained undescribed up to the present time. I am familiar with the males of only two of the six species.

KEY TO SPECIES OF SUBGENUS *RHABDEPYRIS*

Females

1. Front angle of ocellar triangle less than a right angle (as in Fig. 1) 2
   Front angle of ocellar triangle a right angle or slightly greater (as in Fig. 2) 4
2. Coxae and femora wholly bright rufo-castaneous; propodeum with nine discal carinae; front femora robust, about 2.3 x as long as wide .... 1. *mellipes* n. sp.
   Coxae and femora wholly brown or black; propodeum with seven discal carinae; front femora not quite as robust, measuring 2.5-2.7 x as long as wide 3
3. LFW 2.2 mm; scape pale castaneous; antennae elongate, third segment about 1.5 x as long as wide; scutellar groove rather thin and shallow .... 2. *huachucae* n. sp.
   LFW 1.6-1.8 mm; scape blackish except paler apically; antennae short, third segment 1.0-1.2 x as long as wide; scutellar groove relatively wider and deeper .... 3. *muesebecki* n. sp.
4. Head rather long and vertex much produced above eye tops; WH 0.93 x LH; WF 1.44 x HE; OOL 1.35 x WOT; a larger species,

LFW 2.0 mm .... 4. *gracilis* n. sp.

Head more nearly circular in anterior view, the vertex only moderately produced above the eye tops (Fig 2); WH 0.98-1.00 x LH; WF not over 1.25 x HE; OOL less than WOT; very small species, LFW under 1.8 mm 5

5. Front very narrow, WF 0.90 x HE; third antennal segment wider than long; scutellar groove wider on the sides than medially; front femora 2.4 x as long as wide .... 5. *minutulus* n. sp.

Front wider, WF 1.23 x HE; third antennal segment longer than wide (Fig. 2); scutellar groove arching, not wider laterally than medially; front femora 2.9 x as long as wide .... 6. *nigriscapus* n. sp.

Males

Front angle of ocellar triangle less than a right angle; head considerably wider than high .... 3. *muesebecki* n. sp.

Front angle of ocellar triangle approximately a right angle; WH/LH = 1.0 .... 4. *gracilis* n. sp.

TABLE I. SUMMARY OF SOME CHARACTERS OF FEMALES OF SUBGENUS RHABDEPYRIS

Species	Locality	LFW (mm.)	WH/LH	WF/HE	OOL/WOT	Propodeal carinae	Front angle ocellar triangle (degrees, approximate)
1. mellipes	Fla. (type)	2.0	1.00	1.15	1.33	9	70
2. huachucae	Ariz. (type)	2.2	0.92	1.06	1.15	7	80
3. muesebecki	Honduras (type)	1.8	1.01	1.12	1.30	7	70
	"Mexico"	1.7	0.98	1.27	1.30	7	80
	Guerrero	1.6	0.95	1.12	1.36	7	80
	Costa Rica	1.8	0.96	1.09	1.15	7	80
	Bolivia	1.7	1.00	1.09	1.16	7	80
4. gracilis	Calif. (type)	2.0	0.93	1.44	1.35	7	90
5. minutulus	Peru (type)	1.3	1.00	0.90	0.80	7	90
6. nigriscapus	Argentina (type)	1.7	0.98	1.23	0.87	9	100

1. RHABDEPYRIS (RHABDEPYRIS) MELLIPES new species

Holotype. — ♀, FLORIDA: Orange Co., 22 March 1930 (J. E. Sadler, Fla. Fruit Fly Trap Survey) [USNM, No. 67,535].

Description of female type. — Length 3.0 mm; LFW 2.0 mm. Black; palpi and mandibles testaceous, the latter with the teeth rufous; antennae pale castaneous, the flagellum somewhat dull; tegulae testaceous; legs pale rufo-castaneous except the front and hind coxae somewhat infuscated; wings subhyaline. Clypeus obtusely angulate, more sharply angled on the midline, the median carina strong, arched in profile. WH/LH = 1.0; front narrow, WF .57 x WH, 1.15 x HE; front angle of ocellar triangle less than a right angle; OOL 1.33 x WOT (Fig. 1). Vertex broadly rounded off a considerable distance above eye tops, distance from eye tops to vertex crest equal to slightly more than half HE. Front strongly alutaceous, somewhat shining, punctures shallow and inconspicuous, separated by 2 – 4 x their own diameters. First four antennal segments in a ratio of about 20:6:6:7, segment three (like the following segments except the last) very slightly longer than thick.

Pronotal disc 1.6 x length of mesoscutum along the midline, its posterior margin paralleled by a series of large but shallow foveae; pro- and mesonota alutaceous and shallowly punctate like the front; notauli narrowly tear-shaped, diverging in front; scutellar groove quite broad, deflected backward but not enlarged at each end. Propodeal disc 1.2 x as wide as its median length; disc with numerous longitudinal carinae, of which three are complete, six others nearly so; surface aside from the carinae transversely striate; surface of declivity and side-pieces somewhat beaded. Front femora 2.3 x as long as wide.

Remarks. — This species is known only from the type. It is the only member of this complex with pale legs.

2. RHABDEPYRIS (RHABDEPYRIS) HUACHUCAE new species

Holotype. — ♀, ARIZONA: Cochise Co., Huachuca Mts., Ramsey Canyon, 22 March 1956 (F. G. Werner & G. D. Butler) [MCZ, No. 30,936].

Description of female type. — Length 4.0 mm; LFW 2.2 mm. Black; palpi and mandibles testaceous, the latter with the teeth rufous; scape pale castaneous, flagellum dull, light brown below but much darker on the upper side; tegulae testaceous; coxae and hind femora black; front femora and to a lesser extent the middle femora suffused with blackish toward the middle, the legs otherwise pale castaneous; wings hyaline, the veins and stigma light brown. Clypeus somewhat rounded except with a small median tooth formed by the tip of the strong, arched median ridge. Head higher than wide, WH .92 x LH; front narrow, WF .59 x WH, 1.06 x HE; front angle of ocellar triangle slightly less than a right angle, OOL 1.15 x WOT. Vertex rounded off a distance above eye tops equal to slightly more than half HE. Front strongly alutaceous, somewhat shining below but rather dull at the ocellar triangle; punctures very small, separated by 2 – 4 x their own diameters.

First four antennal segments in a ratio of about 26:9:10:12, segment three 1.6 x as long as wide, all flagellar segments considerably longer than wide.

Pronotal disc 1.6 x as long as mesoscutum along the midline, its posterior margin paralleled by a shallow, weakly foveolate groove; surface of pro- and mesonota uniformly alutaceous, obscurely punctate; notauli slender, slightly attenuate and divergent anteriorly; scutellar groove forming an arc. Propodeal disc 1.18 x as wide as its median length; disc with five parallel carinae, also two additional weaker carinae beside the median carina, otherwise transversely striate; declivity beaded, weakly striate below; side-pieces wholly beaded. Front femora 2.7 x as long as wide.

Remarks. — This species is known only from the type.

3. Rhabdepyris (Rhabdepyris) muesebecki new species

Holotype. — ♀, HONDURAS: intercepted at quarantine on banana debris from Honduras, at Galveston, Texas, 18 February 1935 (C. P. Trotter; No. 887) [USNM, No. 67,536].

Description of female type. — Length 3.4 mm; LFW 1.8 mm. Black; palpi light brown; mandibles testaceous except infuscated at extreme base; scape black except apical .3 pale castaneous like the following segment, remainder of antenna dark castaneous on upper side, light yellowish brown below; tegulae light brown; coxae and femora dark brown, legs otherwise testaceous; wings hyaline, veins and stigma very pale. Clypeus prominent, obtusely subangulate except with a small acute median angulation; median carina high, arched. Head slightly wider than high, WH 1.01 x LH; front rather narrow, WF .58 x WH, 1.12 x HE; ocelli small, front angle of ocellar triangle less than a right angle, OOL 1.30 x WOT. Vertex broadly rounded off a distance above eye tops equal to about half HE. Front evenly alutaceous although moderately shining, punctures shallow but rather distinct, separated by 2 – 4 x their own diameters. First four antennal segments in a ratio of about 19:6:6:7, segment three 1.1 x as long as thick, segment eleven not longer than thick.

Pronotal disc 1.4 x as long as mesoscutum; posterior margin of disc paralleled by a row of foveae; pro- and mesonota less strongly alutaceous and much more shining than the front. Notauli tear-shaped, diverging toward the front; scutellar groove curved backward and slightly widened on each end. Propodeal disc 1.20 x as wide as its median length, its features exactly as described for the preceding species; declivity and side-pieces uniformly alutaceous, somewhat shining. Front femora 2.5 x as long as wide.

Allotype. — ♂, HONDURAS: La Ceiba, 21 March 1916 (F. J. Dyer) [USNM].

Description of male allotype. — Length 2.0 mm; LFW 1.7 mm. Black; palpi and mandibles pale, as in female; antennae wholly dark brown, scape almost black; legs dark brown, except front tibiae and tarsi testaceous; wings hyaline, veins and stigma brownish. Clypeus angulate, the median ridge subangulate in profile. Eyes prominent; head wider than high, WH 1.07 x LH; front fairly broad, the eyes convergent below, WF .61 x WH, 1.35 x HE; front angle of ocellar triangle slightly less than a right angle; OOL 1.20 x WOT. Front strongly alutaceous, rather weakly shining, with shallow punctures distributed about as in female. Antennae elongate, first four segments in a ratio of about 13:5:9:11, segment three 1.6 x as long as wide, segment eleven 1.9 x as long as wide.

Thoracic dorsum somewhat more shining and less alutaceous than the front; foveolate groove of pronotum, notauli, and scutellar groove all essentially as in female. Propodeal disc 1.2 x as wide as its median length, with five discal carinae and distinct lateral and sublateral carinae, otherwise transversely striate; side-pieces alutaceous, somewhat shining.

Paratypes. — MEXICO: 1 ♀, with tomato, 30 August 1943, intercepted at quarantine at Brownsville, Texas, 54653, lot no. 43-11640 [USNM]; 1 ♂, "San Rafael Jicoltepec" (? = Jilotepec) [USNM]; 1 ♂, 3-6 mi. S Cuernavaca, Morelos, 4000 feet, 17 April 1959 (H. E. Evans) [MCZ]; 1 ♀, Chilpancingo, Guerrero, 4600 feet, June (H. H. Smith) [BMNH]. COSTA RICA: 1 ♀, San José, 1940 (H. Schmidt) [Sec. Agri., São Paulo, Brazil]. BOLIVIA: 1 ♀, Espia, Rio Bopi, July (W. M. Mann; Mulford Exped., 1921-22) [USNM].

Variation. — The paratypes show only insignificant variation in size (LFW 1.6-2.0 mm). The Morelos male has the legs rather pale, all the tarsi being testaceous, the tibiae only partially infuscated; otherwise there is little variation in color. There is a certain amount of variation in head shape and width of the front, the Mexican female taken at Brownsville having a considerably broader front than any other; the Costa Rica and

Bolivia females have the narrowest front and also have the lateral ocelli less far removed from the eye margins (Table I). The propodeum shows little variation in shape or sculpturing. It is conceivable, though I think not probable, that I am confusing more than one species under one name.

4. Rhabdepyris (Rhabdepyris) gracilis new species

Holotype. — ♀, CALIFORNIA: Sacramento, 25 August 1932 (no collector given) [CAS].

Description of female type. — Length 3.2 mm; LFW 2.0 mm. Black, except last abdominal segment suffused with dark reddish brown; palpi light brown; mandibles testaceous on apical half; scape dark brown, paler apically, flagellum castaneous, darker on upper side than below; tegulae light brown; coxae and femora dark brown, legs otherwise light brown; wings hyaline, veins and stigma light brown. Clypeus obtusely angulate except acute at the midline; median carina low except subangularly produced toward the base. Head higher than wide, WH .93 x LH; front broad, WF .66 x WH, 1.44 x HE; ocelli small, in a rather broad triangle, the front angle approximately a right angle; OOL 1.35 x WOT. Vertex produced well above eye tops, distance from eye tops to vertex crest equal to over two-thirds x HE. Front strongly alutaceous although moderately shining, the punctures small and shallow, separated by 2-3 x their own diameters. First four antennal segments in a ratio of about 19:7:7:8, segment three about 1.3 x as long as thick, segment eleven barely longer than thick.

Pronotal disc 1.35 x as long as mesoscutum, its posterior margin paralleled by a foveolate groove; surface of pro- and mesonota moderately shining, obscurely punctate; notauli strong on posterior half of mesoscutum, tapering and diverging anteriorly; scutellar groove rather wide, deflected backward but barely widened on each side. Propodeal disc 1.10 x as wide as long, with seven discal carinae, otherwise transversely striate; declivity and side-pieces beaded. Front femora 2.8 x as long as wide.

Allotype. — ♂, MEXICO: 10 mi. W Durango, Durango, 12 July 1954 (J. W. MacSwain) [CAS].

Description of male allotype. — Length 2.7 mm; LFW 1.9 mm. Black; palpi brown; mandibles testaceous on apical third, the teeth rufous; scape black, flagellum dark brown; legs dark brown; wings hyaline. Clypeus broadly subangulate, with a small median tooth; median ridge arched in profile. WH/LH = 1.0; front broad, WF .64 x WH, 1.42 x HE; front angle of ocellar triangle very slightly exceeding a right angle; OOL 1.33 x WOT; vertex broadly rounded off a considerable distance above the eye tops. Front alutaceous and weakly punctate about as in the female. First four antennal segments in a ratio of about 15:5:11:12, segment three 1.8 x as long as wide, segment eleven about twice as long as wide.

Thoracic dorsum weakly alutaceous, obscurely punctate; notauli very short, strong only on the posterior third of the mesoscutum; scutellar groove arcuate, slightly widened on each side. Propodeal disc 1.1 x as wide as long, with five longitudinal carinae, somewhat beaded beside the median carina but elsewhere transversely striate; declivity and side-pieces beaded.

Remarks. — This association of the sexes seems probable on the basis of available material, but only a great deal more collecting will solve this matter finally. I have seen only these two specimens assignable to this species.

5. RHABDEPYRIS (RHABDEPYRIS) MINUTULUS new species

Holotype. — ♀, PERU (C.H.T. Townsend Coll.) (no further data) [USNM, No. 67,537].

Description of female type. — Length 1.9 mm; LFW 1.3 mm. Head and thorax black; abdomen dark castaneous; palpi and mandibles testaceous; scape and following two antennal segments testaceous, remainder of antenna dark brown except somewhat paler on the under side; coxae and femora dark brown, middle and hind tibiae medium brown, legs otherwise testaceous; wings hyaline, veins and stigma light amber. Clypeus obtusely angulate, with small median tooth. WH/LH = 1.0; front very narrow, WF .53 x WH, .90 x HE; ocelli in a broad triangle, front angle about a right angle; OOL .80 x WOT. Vertex rounded off a short distance above the eye tops, distance from eye tops to vertex crest equal to less than one-third x HE. Front strongly shining below, more weakly shining and strongly alutaceous above; punctures indistinct. First four antennal segments in a ratio of about 14:5:2:4, segments three and eleven both wider than long.

Pronotal disc 1.3 x as long as mesoscutum, its posterior margin paralleled by a rather weak series of small foveae; surface moderately shining, obscurely punctate. Mesoscutum with the notauli strong on the posterior half; scutellar groove fairly wide, wider on the sides than medially. Propodeal disc 1.14 x as wide as long, with five longitudinal carinae and two additional, weaker carinae beside the median carina, otherwise transversely striate; declivity and side-pieces shining, rather weakly alutaceous. Front femora 2.4 x as long as wide.

6. Rhabdepyris (Rhabdepyris) nigriscapus new species

Holotype. — ♂, ARGENTINA: 5 mi. N Jujuy, 15 February 1951 (Ross & Michelbacher) [CAS].

Description of female type. — Length 2.6 mm; LFW 1.7 mm. Black; palpi and mandibles testaceous; scape black except paler at tip, antennae otherwise dark brown above, light brown on under side; coxae and femora dark brown, legs otherwise pale castaneous; wings hyaline, veins and stigma light brown. Clypeus broadly rounded apically, with a small median tooth. WH .98 x LH; front of moderate width, WF .64 x WH, 1.23 x HE; ocelli in a broad triangle, OOL .87 x WOT (Fig. 2). Distance from eye tops to vertex crest equal to slightly less than half HE. Front rather strongly alutaceous, somewhat shining, with small, shallow punctures which are separated by 3 – 5 x their own diameters. First four antennal segments in a ratio of about 19 :7 :6 :7, segments three and eleven both about 1.2 x as long as wide.

Thoracic dorsum alutaceous, moderately shining, obscurely punctate; pronotal disc 1.2 x as long as mesoscutum, its posterior margin paralleled by a rather strong series of foveae. Notauli very short, barely longer than wide; scutellar groove arching, not wider on the sides than medially. Propodeal disc 1.10 x as wide as long, with five longitudinal carinae between which are four other, weaker carinae, otherwise transversely striate; declivity weakly transversely striate; side-pieces somewhat beaded. Front femora 2.9 x as long as wide.

Remarks. — This species is similar to the preceding in many ways, but there are so many minor differences that the two are unlikely to be conspecific. Both species are known from the types only.

B. Subgenus TRICHOTEPYRIS Kieffer

Trichotepyris Kieffer, 1906, *in* André, Spec. Hymen. Eur., 9: 376 (type species: *R. pallidipennis* Kieffer, 1906; designated by Muesebeck & Walkley, 1950) (proposed as subgenus of *Rhabdepyris*). — Kieffer, 1914, Das Tierreich, 41: 346 (placed in synonymy of *Rhabdepyris*).

Subgeneric characters. — Small to medium-sized bethylids; black, head and thorax sometimes with metallic reflections, abdomen sometimes brownish or in part rufous; eyes densely clothed with short hairs; body with short, fine, mostly pale hair, without the strong dark setae of the preceding group (exception: *nigropilosus*); middle tibiae with or without spines. Mandibles large, in the male terminating in five sharp teeth, in the female with four or five teeth of variable development; base of mandibles fairly close to bottoms of eyes, malar space less than or about equal to width of mandibles at their base (exception: *nigropilosus*); male with third antennal segment very small, shorter than second segment, closely consolidated with the much larger fourth segment. Pronotum moderately long, with or without a foveolate groove paralleling its posterior margin; notauli usually complete or nearly so; scutellar groove strong; propodeum of variable shape, with from three to seven longitudinal carinae, with or without transverse striations; declivity and side-pieces with fine striations in most species. Mesopleurum with an elongate upper fovea (sometimes divided) and a large lower fovea which is often incomplete above. Claws dentate, the tooth distinct, erect or sloping outward to some extent.

Remarks. — I have not seen the type species of *Trichotepyris* and may or may not be employing the name correctly. The type, from Hungary, has hairy eyes and seems to agree well enough with the American species so far as the description goes, although it is only 3 mm long, which is close to the minimum for our species. The above diagnosis is based entirely on the American species. One species, *nigropilosus,* is intermediate in its characters between this and the preceding subgenus.

KEY TO SPECIES OF SUBGENUS *TRICHOTEPYRIS*

Females

1. Wings fully developed and unbanded (occasionally somewhat more clouded around radial vein than elsewhere); propodeal disc at least 1.15 x as wide as long 2

Wings either (a) very short, not reaching the abdomen, or (b) strongly twice-banded, the bands separated by a subhyaline streak at the stigma; small, elongate species, the propodeal disc at most 1.10 x as wide as long (*Pulchripennis* group) 12

2. Body setae coarse, fuscous; veins on basal half of fore wing bearing dark setae which are much larger than the setulae on the wing membrane; side-pieces of propodeum wholly beaded; LFW not over 2.1 mm (*Nigropilosus* group) .... 7. *nigropilosus* n. sp.

Body setae fine, pale; veins of fore wing bearing pale setae little if any longer than those on the membrane; side-pieces of propodeum at least in part striolate or aciculate (*Megacephalus* group) 3

3. Antennal scrobes carinate; head very broad, WH at least 1.12 x LH (Fig. 4); propodeal disc at least 1.5 x as wide as long 4

Antennal scrobes not at all carinate; head not as broad, WH at most 1.04 x LH (Figs. 5, 6); propodeal disc variable 5

4. Mandibles very large and protuberant, their outer margins strongly rounded, the fourth tooth much broader than the adjacent teeth (Fig. 43); WF 1.45-1.65 x HE .... 8. *megacephalus* (Ashmead)

Mandibles less prominent, the lower margin much less strongly rounded, the fourth tooth only slightly wider than adjacent teeth (Fig. 44); WF about 1.40 x HE .... 9. *werneri* n. sp.

5. Lower mesopleural fovea well defined, either completely enclosed or with the upper margin indistinct on the middle third (Figs. 27, 28); front narrow, WF 0.95-1.20 x HE 6

Lower mesopleural fovea poorly defined above, the upper margin very broadly incomplete (as in Figs. 25, 26); front variable 8

6. Front very narrow, WF slightly less than HE; OOL 1.2 x WOT; front femora moderately robust, about 2.1 x as long as wide .... 16. *subaeneus* Kieffer

Front somewhat broader, WF slightly exceeding HE (Figs. 6, 7); OOL 1.3-1.4 x WOT; front femora more slender, 2.3-2.5 x as long as wide 7

7. Lower mesopleural fovea completely enclosed (Fig. 28); head and thorax strongly reflecting green or blue-green .... 15. *carolinianus* n. sp.

Lower mesopleural fovea with its upper margin indistinct on the middle third (Fig. 27); head and thorax at most faintly aeneous or violaceous .... 11. *texanus* n. sp.

8. Lower part of lower mesopleural fovea with some longitudinal striae (Fig. 26); front extremely broad, WF 1.7-1.8 x HE; clypeus rounded or subtruncate apically (Fig. 5) .... 10. *apache* n. sp.

Lower mesopleural fovea without striae; front less broad, WF not more than 1.4 x HE 9

9. Head much longer than wide, WH 0.91 x LH (Fig. 8); front femora somewhat swollen, their length about 1.9 x their maximum width; cutting edge of mandibles unusually strongly oblique (Fig. 48) .... 17. *angusticeps* n. sp.

Head slightly wider than long, WH 1.02-1.03 x LH; front femora more slender, 2.1-2.4 x as long as wide; cutting edge of mandibles less strongly oblique 10

10. Front narrow, WF about 1.10 x HE; propodeum elongate, the disc 1.2 x as wide as long, wholly covered with transverse striae; a minute species, LFW 2.2 mm . . . . .19. *plaumanni* n. sp.

Front moderately wide, WF 1.25-1.35 x HE; propodeum shorter, the disc 1.3-1.5 x as wide as long, polished and almost without sculpturing on the sides; LFW 2.4-3.0 mm 11

11. Third antennal segment distinctly longer than wide; legs beyond coxae light castaneous; scutellar groove very thin medially, connecting a pair of round pits . . . . 12. *mexicanus* n. sp.

Third antennal segment wider than long (Fig. 9); femora dark brown; scutellar groove strong, arching, only slightly widened on each side; front femora only 2.1 x as long as wide . . 13. *fortunatus* n. sp.

12. Wings very short, not reaching posterior margin of propodeum; propodeal disc elongate, as long as or slightly longer than wide; OOL 1.4-1.8 x WOT . . . . 23. *amabilis* Fouts

Wings fully developed; propodeal disc slightly wider than long; OOL 1.25-1.45 x WOT 13

13. Head slightly wider than high, WH 1.03 x LH; WF 1.08 x HE; posterior margin of pronotum not paralleled by a punctate groove . . . . 20. *pulchripennis* n. sp.

Head higher than wide, WH 0.92-0.93 x LH; WF 0.88-0.95 x HE; posterior margin of pronotum paralleled by a strong, punctate groove 14

14. Side-pieces of propodeum shining, very finely aciculate; OOL 1.40 x WOT . . . . 21. *iridescens* n. sp.

Side-pieces of propodeum less shining, with well-defined longitudinal striae which curve upward posteriorly; OOL 1.25-1.35 x WOT . . . . 22. *cupreolus* n. sp.

Males

1. Head transverse, very much wider than high (WH at least 1.12 x LH) (Fig. 17); WF at least 1.30 x HE; propodeal disc at least 1.40 x as wide as its median length 2

Head subcircular, at most slightly wider than high (WH not more than 1.08 x LH) (Fig. 18); front and propodeal disc not usually as wide as above 4

2. Antennal scrobes not carinate; scutellar groove very thin; OOL about 1.2 x WOT; lower mesopleural fovea somewhat striate below . . . . .10. *apache* n. sp.

Antennal scrobes margined by weak carinae which do not reach the eye margins (Fig. 17); scutellar groove wider; OOL and WOT subequal; lower mesopleural fovea without striations 3

3. Propodeum very short, the disc 1.45 to 1.65 x the median length, more or less smooth and polished on the sides behind ....8. *megacephalus* (Ashmead)
   Propodeum somewhat longer, the disc 1.40 x as wide as the median length, the surface with fine transverse striations except at the extreme posterior margin ....9. *werneri* n. sp.
4. Antennal scrobes weakly carinate; front and thoracic dorsum olive-green; propodeal disc only slightly wider than long, the width about 1.15 x the median length ....18. *olivaceus* n. sp.
   Antennal scrobes not at all carinate; front and thoracic dorsum not or but weakly or in small part olive-green; propodeal disc variable ...5
5. Femora wholly bright rufo-testaceous; scape rufo-testaceous; LFW 3.4 mm; front narrow, WF 1.16 x HE ....14. *lupus* n. sp.
   Femora more or less brownish, dull; scape brownish or black; LFW 2.2-3.2 mm 6
6. Median lobe of clypeus strongly angulate, the angle slightly greater than a right angle except the tip acute; WH 0.98 x LH; propodeal disc wholly covered with rather strong transverse striae ....19. *plaumanni* n. sp.
   Median lobe of clypeus broader, obtusely sub-angulate or somewhat rounded, usually with a median tooth, WH 1.00-1.08 x LH; propodeal disc with the striae obsolescent at least posteriorly 7
7. Front strongly beaded, rather dull; propodeum strongly alutaceous, its posterior margin paralleled by a strong row of foveae; OOL 1.25-1.45 x WOT; side pieces of propodeum weakly or incompletely striate ....23. *amabilis* Fouts
   Front alutaceous or moderately beaded, somewhat shining; foveolate groove along posterior margin of pronotum rather weak; OOL 1.05-1.20 x WOT; side pieces of propodeum completely covered with longitudinal striae 8
8. Propodeum short, disc measuring 1.40-1.50 x as wide as the median length; lower mesopleural fovea not at all defined on its upper side ....12. *mexicanus* n. sp.
   Propodeum longer, disc measuring 1.20-1.35 x as wide as the median length; lower mesopleural fovea defined on the upper side both in front and behind, the margining ridge generally obsolete in the middle part of the fovea ....11. *texanus* n. sp.

TABLE II. SUMMARY OF SOME CHARACTERS OF TYPE SPECIMENS OF SPECIES OF SUBGENUS TRICHOTEPYRIS (♀♀)

Species	LFW (mm)	WH/LH	WF/HE	OOL/WOT	Propodeal disc W/L	Front femora L/W	Antennal scrobes carinate
7. nigropilosus	1.9	1.00	1.00	1.25	1.35	2.5	-
8. megacephalus	3.8	1.15	1.60	1.25	1.70	2.5	+
9. werneri	3.4	1.17	1.40	1.22	1.50	2.7	+
10. apache	4.0	0.94	1.80	1.75	1.60	2.6	-
11. texanus	3.0	0.98	1.10	1.40	1.30	2.5	-
12. mexicanus	3.0	1.02	1.31	1.10	1.50	2.4	-
13. fortunatus	2.4	1.03	1.28	1.23	1.30	2.1	-
15. carolinianus	3.3	0.98	1.10	1.35	1.25	2.4	-
16. subaeneus	2.9	0.92	0.95	1.20	1.25	2.1	-
17. angusticeps	3.0	0.91	1.28	1.75	1.15	1.9	-
19. plaumanni	2.2	1.02	1.10	1.20	1.20	2.3	-
20. pulchripennis	2.6	1.03	1.08	1.45	1.05	2.0	-
21. iridescens	2.6	0.92	0.93	1.40	1.10	2.3	-
22. cupreolus	2.4	0.93	0.95	1.25	1.05	2.4	-
23. amabilis	0.6	0.93	1.05	1.80	1.00	2.3	-

TABLE III. SUMMARY OF SOME CHARACTERS OF TYPE SPECIMENS OF SPECIES OF SUBGENUS TRICHOTEPYRIS (♂♂)[1]

Species	LFW (mm)	WH/LH	WF/HE	OOL/WOT	Propodeal disc W/L	Antennal seg. 4 L/W	Antennal scrobes carinate
8. megacephalus	3.0	1.15	1.40	0.96	1.60	2.0	+
9. werneri	2.9	1.15	1.33	0.92	1.40	2.2	+
10. apache	3.4	1.12	1.45	1.20	1.60	2.2	-
11. texanus	2.8	1.04	1.25	1.06	1.20	2.4	-
12. mexicanus	2.5	1.07	1.35	1.06	1.45	1.9	-
14. lupus	3.4	1.01	1.16	1.23	1.33	2.4	-
18. olivaceus	2.5	1.00	1.14	1.16	1.15	2.5	+
19. plaumanni	2.3	0.98	1.22	1.15	1.15	2.5	-
23. amabilis	2.3	1.00	1.35	1.45	1.35	2.5	-

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[1] The specimens treated here are either holotypes (lupus, olivaceus), allotypes (werneri, apache, texanus, mexicanus, plaumanni), or plesiallotypes (megacephalus, amabilis). The males of eight species are unknown.

NIGROPILOSUS SPECIES-GROUP

Here I assign a single species which is intermediate in its characters between this and the preceding subgenus. The eyes are hairy, but the setae on the body and wing veins resemble those of *Rhabdepyris, sensu stricto.* It is known from females only, and it is possible that the male antennae, when known, will indicate that the species is better placed in *Rhabdepyris, sensu stricto.*

7. RHABDEPYRIS (TRICHOTEPYRIS) NIGROPILOSUS new species

Holotype. — ♀, PANAMA: Barro Colorado Island, Canal Zone, Jan. 1960 (W. L. Brown & E. S. McCluskey) [MCZ, No. 30,938].

Description of female type. — Length 2.7 mm; LFW 1.9 mm. Body black, without metallic reflections; palpi and mandibles wholly straw-colored; antennae light brown except basal two-thirds of scape dark brown; tegulae light brown; coxae black. femora dark brown on outer surface, legs otherwise testaceous; wings hyaline, veins and stigma brownish. Head and thorax with an abundance of black setae of moderate length, most of them directed strongly backward; legs also with dark setae, some of those on the tibiae fully erect; major wing veins with dark setae larger than those on the membrane; abdomen with scattered setae ventrally and apically. Mandibles with five teeth, the basal three teeth small, sharp. Clypeus with its median lobe moderately prominent, rounded, with a small median tooth formed by the end of the median carina, which is low although subangulate toward its base. WH/LH = 1.0; front narrow, WF .57 x WH, 1.0 x HE; front angle of ocellar triangle much less than a right angle, OOL 1.25 x WOT. Antennal scrobes not carinate; vertex smoothly rounded off a very short distance above the eye tops. Front shining, moderately alutaceous, the punctures numerous and fairly large, but so shallow as to barely interrupt the surface. Antennae compact, first four segments in a ratio of about 21:6:7:7, segment three barely longer than wide, outer flagellar segments (except the last) slightly wider than long. (Fig. 3.)

Pronotal disc rather short and broad, along the midline 1.3 x as long as mesoscutum, abruptly margined both in front and on the sides, its posterior margin paralleled by a series of small foveae; surface (like that of the mesoscutum) shining, moderately alutaceous, the punctures shallow and rather indistinct. Notauli diverging and much attenuated anteriorly; scutellar groove strong, deflected backward and slightly expanded on each end. Propodeal disc 1.35 x as wide as its median length, with five straight, complete discal carinae as well as well developed sublateral carinae, the disc also wholly and somewhat irregularly transversely striate; postero-lateral angles foveolate; declivity strongly beaded, without striae, the median carina strong; side-pieces wholly beaded, without striae. Mesopleurum with a rather irregular series of ridges which do not form distinct, depressed foveae. Front femora measuring 2.5 x as long as wide; middle tibiae not at all spinose.

Paratypes. — PANAMA: 2 ♀ ♀, El Valle, November 1946 (N.L.H. Krauss) [USNM]. BRAZIL: 3 ♀ ♀, Nova Teutonia, Santa Catarina, July 1953, September 1957, and February 1964 (F. Plaumann) [MCZ; Coll. G. R. Ferguson].

Variation. — The Panama paratypes resemble the type very closely in size, color, and sculpturing. In both specimens the head is slightly broader than high (WH 1.02 and 1.04 x LH), the front also somewhat broader in relation to the eyes (WF 1.07 and 1.12 x HE); OOL is 1.18 and 1.35 x WOT. The three paratypes from southern Brazil, although from a locality over 3000 miles from the type locality, show no important differences in color or sculpture. All are slightly larger than the Panama specimens (LFW 2.1 – 2.2 mm) and two of them have an unusually broad front (WF 1.30 and 1.50 x HE; OOL 1.25 and 1.40 x HE); in all three specimens the head is slightly wider than high. Presumably this species is widely distributed in South America.

Megacephalus species-group

To this group I assign twelve species, six of them known from only one sex. These species lack the strong, dark setae of the preceding species and also lack the specializations of the wings of the *pulchripennis* group. This is a closely knit group, and the males are rather difficult to separate.

8. Rhabdepyris (Trichotepyris) megacephalus (Ashmead)

Epyris megacephalus Ashmead, 1893, Bull. U.S. Nat. Mus., 45: 61 [Type: ♀, CALIFORNIA: Poway (San Diego Co.) (no further data) (USNM, No. 14,067)].

Rhabdepyris (*Trichotepyris*) *megacephalus* Kieffer, 1908, Genera Insect., 76: 32.

Rhabdepyris (*Rhabdepyris*) *megacephalus* Kieffer, 1914, Das Tierreich, 41: 355.

Rhabdepyris megacephalus Muesebeck and Walkley, 1951, U.S. Dept. Agri., Monogr. 2, p. 729 — Evans, 1964, Bull. Mus. Comp. Zool., 132, figs. 63-67.

Description of female type. — Length 6.5 mm; LFW 3.8 mm. Black, except as follows: pronotal collar ferruginous; apical abdominal segment castaneous; palpi straw-colored; mandibles ferruginous; antennae rather uniformly light castaneous; tegulae testaceous; legs bright castaneous except front coxae blackish; wings subhyaline, veins and stigma amber. Mandibles very stout, their outer margins very strongly rounded; apical margin broad, the outer two teeth acute, the third tooth broad and short but subacute, the fourth tooth very broad and truncate, the fifth (basal) tooth small, rounded, and weakly separated from the fourth tooth (Fig. 43). Clypeus very short, very broadly and weakly subangulate, the median carina subangulate in profile. Head very broad, 1.15 x as wide as high; front very broad, WF .67 x WH, 1.60 x HE; ocelli small, widely spaced, front angle of ocellar triangle slightly less than a right angle, OOL 1.25 x WOT. Antennal scrobes carinate, the carinae not nearly reaching the eye margins; sides of head roundly convergent behind the eyes, the vertex straight across, distance from eye tops to vertex crest about two-thirds x HE; head strongly developed behind the eyes, in lateral view the temples somewhat wider than the eyes. Front strongly shining, weakly alutaceous, with abundant punctures which are separated by 1 – 2 x their own diameters. Scape long and curved; first four antennal segments in a ratio of about 26:6:5:7, segment three 1.25 x as long as its maximum width.

Pronotal disc sloping very gradually to the collar, sides of disc more abruptly rounded; collar rugulose; disc shining, weakly alutaceous, with small punctures; median length of pronotal disc about twice that of mesoscutum; pronotum with a weak depression paralleling the posterior margin. Mesoscutum and scutellum alutaceous, more so than the pronotum and much more so than the front, punctures smaller than those of the pronotum but well distributed; notauli linear, diverging toward the front; scutellar groove relatively wide and short, broadened and deflected backward on each side. Propodeum very short, the disc 1.7 x as wide as the median length; disc with five longitudinal carinae and some vague indication of other carinae between them, also transversely ridged between the carinae; postero-lateral portion of disc smooth and polished; sublateral carinae absent; side-pieces longitudinally striolate. Mesopleurum weakly alutaceous and punctate, the lower fovea incomplete above. Front femora 2.5 x as long as wide; middle tibiae very weakly spined above.

Plesiallotype. — ♂, ARIZONA: Tucson, 13 June 1938 (R. H. Crandall) [MCZ].

Description of male plesiallotype. — Length 4.0 mm; LFW 3.0 mm. Head and thorax black, faintly aeneous; abdomen piceous, fading to dark reddish brown apically; palpi straw-colored; mandibles blackish except apical .2 testaceous, the teeth rufous; antennae very dark brown except fading to medium brown at the apex; tegulae testaceous; coxae dark brown, femora medium brown, trochanters, tibiae, and tarsi light brown; wings hyaline, veins and stigma amber. Clypeus broadly rounded, with a small angulation formed by the end of the median carina, the latter very strongly arched in profile. Head broad, 1.15 x as wide as high; WF .64 x WH, 1.40 x HE; ocelli in about a right triangle, OOL .96 x WOT. Antennal scrobes carinate, the carinae not reaching the eye margins; vertex straight across, distance from eye tops to vertex crest equal to about one-third x HE. Front strongly alutaceous, weakly shining, the punctures numerous but shallow and inconspicuous. First four antennal segments in a ratio of about 12:3:2:8, segment four 2.0 x as long as wide, segment eleven 2.2 x as long as wide.

Pronotal disc gradually rounded to the plane of the collar, more abruptly rounded on the sides, the disc alutaceous and very slightly more shining than the front; disc 1.4 x as long as mesoscutum along the midline, its posterior margin paralleled by a distinct, foveolate groove. Mesoscutum moderately shining, with distinct, small punctures; notauli linear, strongly diverging toward the front; scutellar groove strong, roundly expanded on each side. Propodeal disc 1.6 x as wide as long, with five longitudinal carinae between which it is somewhat rugulose, postero-lateral portion smooth and polished; side-pieces longitudinally striolate. Mesopleurum alutaceous, moderately shining, lower fovea not well defined above.

Specimens examined. — CALIFORNIA: 1 ♀, Poway, San Diego Co. [type, USNM]; 1 ♀, Imperial Co., 29 May 1912 (On *Helianthus*, J. C. Bridwell) [USNM]; 1 ♀, Mojave Desert, Aug. 1937 (R. H. Smith) [USNM]. ARIZONA: 1 ♀, 2 ♂♂, Tucson, June [USNM, MCZ]; 1 ♀, 5 mi. W Portal, May (M. Statham) [AMNH]; 1 ♀, Marana, July (F. Werner) [UA]; 1 ♀, Tubac, June (T. Dees) [UA]; 1 ♀, Huachuca, 1937 (W. Benedict) [KU]; 1 ♀, 1 ♂, Sahuarita, July (G. Butler) [MCZ]; 1 ♀, Oracle Jct., Pinal Co. (F. Werner) [MCZ]; 1 ♀, Empire Mts., 5000 feet, May (A. Nichol) [UA]; 1 ♀, 2 ♂♂, Santa Rita Mts., May, July [CAS, KU]; 1 ♀, McNeal, July (C. Williams) [UA]; 1 ♀, Elfrida, July (A. Telford) [UA]; 1 ♂, Maricopa, June (G. Butler) [UA]; 2 ♂♂, 15 mi. W Ft. Apache, June (Butler & Werner) [UA, MCZ]; 1 ♂, Avra Val, June [UA]; 1 ♂, Superior, July (G. Butler) [UA]; 2 ♂♂, Arivaca, July [KU]; 2 ♂♂, 30 mi. E Pearce, July (Butler & Werner) [UA, MCZ]; 1 ♂, Continental, July (G. Butler) [UA]; 1 ♂, Theba, July (G. Butler) [UA]; 2 ♂♂, Canelo, July (G. Butler) [UA]. NEW MEXICO: 1 ♂, Florida, July (On *Actinella*, T. Cockerell) [USNM]. TEXAS: 1 ♀, Cooper's Store, Big Bend Park, April (C. Michener) [KU]; 1 ♂, Sierra Blanca, El Paso Co., July [USNM].

Variation. — The females show little variation in size or standard measurements; LFW varies from 2.8 to 3.8 mm; WH from 1.12 to 1.17 x LH; WF 1.45 to 1.62 x HE; propodeal disc from 1.50 to 1.65 x as wide as long. Several specimens have weak aeneous or violaceous reflections on the front and on the thoracic dorsum; several have the middle and hind coxae strongly infuscated, like the front coxae, and two have the femora more or less infuscated. The specimens from Tubac and from McNeal, Arizona, have the front more distinctly alutaceous than any of the others. None of the variation seems closely correlated with geography.

The males are somewhat more variable. LFW varies from 2.3 to 3.3; WH from 1.12 to 1.20 x LH; WF from 1.30 to 1.50 x HE; propodeal disc from 1.45 to 1.65 x as wide as long. Several specimens lack metallic reflections on the head and thorax; the color of the flagellum varies from wholly light castaneous to wholly black; in a few specimens the legs are very dark, only the tarsi being light brown. In some specimens the front and thoracic dorsum are rather dull, in others moderately shining. In no case are the punctures of the front conspicuous, but in several specimens they are more evident than in the plesiallotype. Again, none of the variation seems correlated with geography.

9. Rhabdepyris (Trichotepyris) werneri new species

Holotype. — ♀, ARIZONA: Globe, Gila Co., 3600 feet elevation, 8 July 1949 (mesquite-oak; F. Werner & W. Nutting) [USNM, No. 67,538].

Description of female type. — Length 6 mm; LFW 3.4 mm. Black, except as follows: pronotal collar ferruginous; apical rims of abdominal tergites, and all of apical two tergites, brownish; palpi and tegulae testaceous; mandibles ferruginous; antennae light castaneous, slightly paler below than above; legs light castaneous except front coxae blackish, middle and hind coxae and all the femora weakly suffused with brownish; wings hyaline, veins and stigma amber. Mandibles with the lower margin weakly curved, apex with five teeth in an oblique series, basal two teeth blunt, the fourth tooth only slightly wider than adjacent teeth (Fig. 44). Clypeus very short, the apex very broadly and weakly angulate, the median carina rather broad and ill-defined, not arched or angulate in profile. Head broad, 1.17 x as wide as high; front very broad, WF .67 x WH, 1.40 x HE; front angle of ocellar triangle slightly less than a right angle; OOL 1.22 x WOT. Antennal scrobes carinate, the carinae not reaching the eye margins; distance from eye tops to vertex crest equal to about half the eye height; vertex straight across; head wide behind the eyes, but the temples slightly less bulging than in *megacephalus*. Front alutaceous, moderately shining, punctures separated by 1-2 x their own diameters. First four antennal segments in a ratio of about 40:10: 9:9, segment three 1.35 x as long as its maximum width. (Fig. 4.)

Pronotal disc sloping very gradually in front, sides more abruptly rounded; collar weakly rugulose; disc 1.65 x median length of mesoscutum; surface alutaceous and punctate about like the front; posterior margin paralleled by a weak depression which contains a series of fairly large punctures. Mesoscutum and scutellum alutaceous like the pronotum, but with somewhat weaker punctures; notauli linear, strongly diverging toward the front; scutellar groove narrow, bent backward but not notably broadened on each side. Propodeum longer than in *megacephalus*, the disc measuring 1.5 x as wide as the median length; disc with five longitudinal carinae and some less distinct carinae between them, also transversely striolate except toward the posterior margin; side-pieces strongly longitudinally striolate. Mesopleurum alutaceous, weakly punctate, the upper fovea complete but the lower fovea not at all defined above (Fig. 25). Front femora 2.7 x as long as wide; middle tibiae with several small spines above.

Allotype. — ♂, ARIZONA: 19 mi. N Globe, Gila Co., 20 June 1957 (mesquite; F. Werner & G. Butler) [MCZ].

Description of male allotype. — Length 3.5 mm; LFW 2.9 mm. Black, except as follows: palpi and tegulae light brown; tips of mandibles rufous; flagellum dark brown, fading to medium brown apically; middle and hind coxae and all femora dark brown, tibiae light brown, tarsi testaceous; wings hyaline, veins and stigma amber. Clypeus obtusely angulate, with a small median tooth formed by the end of the median carina, the latter high and arched. Head broad, 1.15 x as wide as high; WF .65 x WH, 1.33 x HE; ocelli in about a right triangle, OOL .92 x WOT. Antennal scrobes carinate, the carinae not nearly reaching the eye margins; vertex passing nearly straight across a short distance above eye tops. Front rather strongly alutaceous although moderately shining, punctures weak. First four antennal segments in a ratio of about 18:5:3:15, segment four 2.2 x as long as wide, segment eleven twice as long as its maximum width. (Fig. 17.)

Pronotal disc 1.3 x as long as mesoscutum along midline, the surface alutaceous about like the front; posterior margin paralleled by a shallow, obscurely punctate groove. Mesoscutum also alutaceous, moderately shining, obscurely punctate; notauli linear, diverging toward the front; scutellar groove widened and turned backward on each side. Propodeal disc 1.4 x as wide as long, with five longitudinal carinae, the more lateral ones rather short, the surface obliquely striolate laterad of the three median carinae, elsewhere transversely striolate except smooth and polished on the posterior .2 of the disc; side-pieces longitudinally striolate. Mesopleurum moderately shining, the lower fovea open above.

Paratype. — ARIZONA: 1 ♀, Sahuarita, Pima Co., 5 July 1956 (swept from cotton, G. D. Butler) [MCZ].

Variation. — The paratype is smaller than the type (LFW 2.9 mm) and shows faint coppery reflections on the head and thoracic dorsum. It is closely similar to the type in color and sculpturing. WF is .66 x WH, 1.39 x HE; OOL is 1.15 x WOT; the propodeal disc is 1.45 x as wide as high.

10. RHABDEPYRIS (TRICHOTEPYRIS) APACHE new species

Holotype.— ♀, ARIZONA: Continental, Pima Co., 18 August 1960 (sucked from cotton, G. D. Butler) [MCZ, No. 30,-940].

Description of female type.—Length 7 mm; LFW 4 mm. Head and thorax black, thoracic dorsum and to a lesser extent the head with a weak bluish cast; propodeum black; abdomen piceous, the venter and the apical tergite suffused with castaneous; palpi testaceous; mandibles dark ferruginous, infuscated toward the base; scape dark castaneous, infuscated on the upper side throughout; tegulae light brown; legs bright rufo-testaceous except all coxae black, front femora mostly blackish on the lateral surface; fore wings lightly tinged with brownish, veins and stigma amber. Mandibles broad, with five teeth, the basal three teeth somewhat rounded, subequal in size. Clypeus with a strongly projecting median lobe which is rounded apically; median ridge arched near the base, then nearly straight to the apex. Head higher than wide, WH .94 x LH; front broad, WF .72 x WH, 1.80 x HE; ocelli small and well separated, front angle of ocellar triangle less than a right angle, posterior ocelli removed from vertex crest by a distance slightly greater than WOT; OOL 1.75 x WOT, subequal to HE. Head thin, the temples not developed; antennal scrobes not carinate; vertex broadly rounded off far above eye tops, distance from eye tops to vertex crest nearly equal to HE. Front strongly shining, very weakly alutaceous, punctures small although sharply defined, separated by 2-4 x their own diameters. First four antennal segments in a ratio of about 22:5:5:6, segment three 1.2 x as long as its apical width. (Fig. 5.)

Pronotum rather large, along the midline 1.7 x as long as mesoscutum; posterior margin not paralleled by a punctate groove; surface shining but slightly more evidently alutaceous than the front, punctures slightly larger and more widely spaced than on the front. Mesoscutum moderately alutaceous, with small punctures; notauli linear, diverging anteriorly; scutellar groove relatively long and thin, deflected backward at each end but only very slightly enlarged there. Propodeal disc rather short, measuring 1.6 x as wide as its median length; disc with five carinae and two more weak, irregular carinae beside the median carina, otherwise with fine transverse striae except toward the posterior margin; lateral carinae strong, but sublaterals absent; declivity with curved striae which radiate from the median carina; side-pieces longitudinally striolate. Mesopleurum alutaceous, the lower fovea broadly open above, containing some rather distinct longitudinal striae (Fig. 26). Front femora 2.6 x as long as wide; middle tibiae with strong spines above for most of their length.

Allotype. — ♂, MEXICO: La Aduana, Sonora, 22 May 1962 (F. D. Parker & L. A. Stange) [MCZ].

Description of male allotype. — Length 5 mm; LFW 3.4 mm. Black, head and thoracic dorsum very faintly aeneous, tip of abdomen dark reddish brown; palpi light brown; mandibles black, flagellum dark brown; legs pale castaneous except all coxae and femora strongly infuscated (middle femora only slightly infuscated); wings subhyaline, veins and stigma light brown. Clypeus obtusely angulate, the median carina nearly straight in profile. Head broad, 1.12 x as wide as high; front broad, WF .65 x WH, 1.45 x HE; ocelli in about a right triangle, OOL 1.20 x WOT. Antennal scrobes not carinate; vertex broadly rounded off a distance above eye tops equal to less than half HE. Front shining, weakly alutaceous, with strong punctures which are separated by 1-2 x their own diameters. First four antennal segments in a ratio of about 25:7:4:24, segment four 2.2 x as long as wide, segment eleven 2.6 x as long as wide.

Pronotal disc about as long along midline as mesoscutum, narrowly elevated along posterior margin but without a distinct punctate groove; sides of disc rather sharp, front of disc also sloping rather abruptly to the collar; surface alutaceous like the front, the punctures slightly weaker and sparser. Mesonotum as described for female. Propodeal disc 1.6 x as wide as long, features much as in female except the transverse striae more oblique and extending to the transverse carina. Mesopleurum as in female, but the longitudinal striations somewhat weaker.

Paratypes. — ARIZONA: 1 ♀, Avra Val, July-Aug. 1959 (swept from cotton, C. Allen) [USNM]; 1 ♀, Emery Park, Pima Co., 26 July 1956 (swept from cotton, C. Williams) [UA]. MEXICO: 1 ♂, La Aduana, Sonora, same data as allotype [UCD].

Variation. — The female paratypes are smaller than the type (LFW 3.0, 3.5 mm) and lack bluish reflections on the head and thorax. In these two specimens WH is .96 and .97 x LH, WF

1.75 and 1.80 x HE, OOL 1.55 and 1.62 x WOT. In the smaller specimen, the head is less strongly produced behind the eyes, the distance from the posterior ocelli to the vertex crest being slightly less than WOT; in this specimen the striations on the mesopleura are quite weak. The male paratype closely resembles the allotype in size, color, and standard measurements.

Remarks. — Although the male and female here associated are from localities several hundred miles apart, there are certain striking features in common, rendering this sex association highly probable. These include particularly the striae on the mesopleura and the very slender scutellar groove.

11. Rhabdepyris (Trichotepyris) texanus new species

Holotype. — ♀, TEXAS: Big Bend National Park, The Basin, Chisos Mts., 5400 feet, 8-14 July 1948 (oak honeydew, H. E. Evans) [MCZ, No. 30,941].

Description of female type. — Length 4.5 mm; LFW 3.0 mm. Head and thorax black, the front and thoracic dorsum very faintly aeneous; abdomen piceous, slightly paler basally and apically; palpi and tegulae testaceous; mandibles bright ferruginous; scape pale castaneous, flagellum of this color on the under side, somewhat darker on the upper side; legs bright, pale rufo-castaneous except all coxae strongly infuscated; wings subhyaline, veins and stigma amber. Mandibles with five teeth in an oblique series, the basal three teeth rather broad and blunt. Clypeus very short, broadly subangulate apically, the median carina arched in profile. Head slightly higher than wide, WH .98 x LH; front rather narrow, WF .62 x WH, 1.10 x HE; ocelli small, front angle of ocellar triangle less than a right angle; OOL 1.40 x WOT. Antennal scrobes not carinate; temples moderately developed; vertex passing straight across a distance above eye tops equal to less than half HE. Front shining, weakly and uniformly alutaceous, punctures strong, separated by 1-2 x their own diameters. First four antennal segments in a ratio of about 35:9:8:11, segment three 1.15 x as long as its maximum width. (Fig. 6.)

Pronotum 1.5 x as long along midline as mesoscutum, its posterior margin paralleled by a weak, non-foveolate depression; surface shining like the front, the punctures slightly more widely spaced. Mesoscutum and scutellum covered with rather small punctures, surface moderately shining; notauli slender, diverging and becoming gradually attenuated anteriorly; scutellar groove of moderate width, turned backward and slightly expanded on each end. Propodeal disc 1.3 x as wide as its median length; disc with five strong carinae between which are four additional weaker carinae, the disc otherwise wholly covered with fine, transverse striations; side-pieces longitudinally striolate. Mesopleurum alutaceous but moderately shining, with scattered small punctures; upper fovea well formed; lower fovea elongate, well formed except on the middle third of the upper side, where the margin is obsolete (Fig. 27). Front femora 2.5 x as long as wide; middle tibiae with a series of small spines above.

Allotype.— ♂, MEXICO: 8 mi. SE Elota, Sinaloa, 19 May 1962 (F. D. Parker) [MCZ].

Description of male allotype.—Length 3.7 mm; LFW 2.8 mm. Entirely black except as follows: palpi and tegulae light brown; mandibles light brown above and apically, except the teeth rufous; scape black, second and third segments light brown, remainder of flagellum dark brown; legs dark brownish fuscous except the middle and hind tibiae medium brown, the trochanters, front tibiae, and all tarsi testaceous; wings subhyaline, veins and stigma light brown. Clypeus obtusely angulate, with a high median carina which is arched in profile. WH 1.04 x LH; WF .63 x WH, 1.25 x HE; front angle of ocellar triangle less than a right angle, OOL 1.06 x WOT. Antennal scrobes not carinate; vertex very weakly arched, distance from eye tops to vertex crest equal to about one-third x HE. Front strongly alutaceous, moderately shining, obscurely punctate. First four antennal segments in a ratio of about 19:5:3:17, segment four 2.4 x as long as wide, segment eleven 3 x as long as wide. (Fig. 18.)

Pronotal disc about as long along midline as mesoscutum, its posterior margin paralleled by a fairly distinct, obscurely punctate groove; disc moderately shining, with rather weak punctures. Mesoscutum alutaceous, obscurely punctate; notauli and scutellar groove as described for the female. Propodeal disc 1.2 x as wide as long, with five distinct carinae and two other weaker carinae close beside the median carina, disc otherwise with fine transverse striae which are obsolete behind; side-pieces longitudinally striolate. Mesopleurum alutaceous, indistinctly punctate, lower fovea with its upper margin nearly complete, but barely perceptible for much of its length.

Paratypes. — TEXAS: 1 ♀, Brownsville, 21 November 1911, palm jungle sweepings [INHS]; 1 ♀, Cedar Lane, Matagorda Co., 8 September 1928 (J. G. Shaw) [KU]. ARIZONA: 1 ♀, S slope Kitt Pk., Quinlin Mts., Pima Co., 22 April 1961 (M. L. Noller, on composite) [UA]; 1 ♂, S Tucson, 10 June 1962 (F. Werner) [UA]. MEXICO: 2 ♂♂, Rio Yaqui, near Ciudad Obregon, Sonora, 19 May 1957 [ENAC]; 10 ♂♂, 8 mi. SE Elota, Sinaloa, same data as allotype except some 19 April 1962 (L. A. Stange) [UCD, CAS]; 1 ♂, 3 mi. N Alpuyeca, Morelos, 3400 feet, 9 March 1959 (H. E. Evans) [MCZ]

Variation. — In the females LFW varies from 2.5 to 3.1 mm. The two Texas paratypes have the head and thoracic dorsum rather strongly shining and without metallic reflections; the Arizona paratype has these parts rather strongly alutaceous, moderately shining, faintly aeneous-violaceous. WH varies from .96 to .98 x LH; WF varies from 1.10 to 1.18 x HE; propodeum width varies from 1.25 to 1.30 x median length of disc.

The ten male paratypes from Sinaloa show considerable variation in size, color, and sculpture. LFW varies from 2.5 to 3.2 mm. In some specimens the second and third antennal segments are dark like the rest of the antenna, and some variation can be noted in the color of the flagellum and the tibiae. In some specimens the front and thoracic dorsum are strongly alutaceous, almost beaded, while in others these parts are moderately shining and with distinct small punctures; in some specimens the upper margin of the lower mesopleural fovea is apparently only near the anterior and posterior extremities. WH varies from 1.01 to 1.05 x LH, WF from 1.15 to 1.30 x HE; the propodeal disc varies from 1.20 to 1.35 x as wide as long. The two Sonora males show variation in most of these same characters, but are outstanding because of their large size (LFW 3.1-3.3 mm) and because of the fact that the second and third antennal segments are pale castaneous, contrasting strongly with the remainder of the antennae. On the other hand, the Morelos male is small (LFW 2.5 mm), although colored like the Sonora males. In this specimen WH and LH are equal, WF 1.17 x HE, OOL 1.16 x WOT. The Arizona paratype is similar to the allotype in size, color, and standard measurements except that OOL and WOT are equal.

12. Rhabdepyris (Trichotepyris) mexicanus new species

Holotype. — ♀, MEXICO: Nachic, Chiapas [near San Cristobal las Casas], 8000 feet, 27 April 1959 (H. E. Evans) [MCZ, No. 30,942].

Description of female type. — Length 4.2 mm; LFW 3.0 mm. Head and thorax black, with faint olive-green reflections, the pronotal collar dull ferruginous; propodeum black; abdomen black, shining, the last two sternites brownish, the apical tergite mostly testaceous; palpi light brown; mandibles dark ferruginous; antennae wholly rufo-castaneous except apical segments weakly infuscated; tegulae testaceous; legs light rufo-castaneous except all coxae infuscated, front pair nearly black; fore wings lightly tinged with brownish. Mandibles with five teeth, the basal three teeth somewhat rounded. Clypeus obtusely angulate, with a median carina which is weakly arched in profile. Head very slightly wider than high, WH 1.02 x LH; WF .65 x WH, 1.31 x HE; OOL 1.10 x WOT. Antennal scrobes not carinate; vertex broad, nearly straight, distance from eye tops to vertex crest less than half HE. Front shining although moderately alutaceous, the punctures sharply defined, separated by 1.5-2.5 x their own diameters. First four antennal segments in a ratio of about 26:9:8:9, segment three 1.2 x as long as wide.

Pronotal disc only slightly longer than mesoscutum along midline, not sharply margined in front or on the sides; surface somewhat more alutaceous than the front, its punctures slightly more widely spaced; posterior margin paralleled by a weak, nonfoveolate depression. Mesoscutum rather strongly alutaceous, the punctures small but numerous; notauli linear, diverging anteriorly, reaching the anterior margin only as very thin lines; scutellar groove quite thin medially, roundly expanded on each end. Propodeal disc about 1.5 x as wide as its median length, with five distinct carinae and two additional weak carinae closely paralleling the median carina; disc irregularly transversely ridged between the carinae, on the sides finely transversely striolate; declivity with transverse striae, side-pieces with very fine longitudinal striae. Mesopleurum somewhat alutaceous, the lower fovea broadly open above. Front femora 2.4 x as long as wide; middle tibiae very weakly spinose above.

Allotype. — ♂, MEXICO: San Cristobal las Casas, Chiapas, 7500 feet, 26 April 1959 (H. E. Evans) [MCZ].

Description of male allotype. — Length 3.5 mm; LFW 2.5 mm.

Entirely black, the front and thoracic dorsum with a faint bluish cast; palpi light brown; mandibles black except the teeth ferruginous; scape black, flagellum dark brown, fading to medium brown apically; coxae and femora dark brown, tibiae suffused with dark brown basally, legs otherwise light brown; fore wings lightly tinged with brownish. Median lobe of clypeus prominent, somewhat rounded, with a median tooth which is a continuation of the high, arching median carina. WH 1.07 x LH; WF .65 x WH, 1.35 x HE; front angle of ocellar triangle less than a right angle, OOL 1.06 x WOT. Antennal scrobes not carinate; vertex broadly rounded off a short distance above the eye tops. Front rather strongly alutaceous although moderately shining, the punctures small and shallow, separated by 2-4 x their own diameters. First four antennal segments in a ratio of about 16:5:4:12, segment four 1.9 x as long as wide, segment eleven 2.2 x as long as wide.

Pronotal disc very slightly longer along midline than mesoscutum, its posterior margin paralleled by a weakly foveolate groove; disc alutaceous and rather weakly shining like the mesonotum; both pro- and mesonota with numerous but shallow punctures; notauli diverging anteriorly; scutellar groove rather thin, expanded and deflected backward at each end. Propodeal disc 1.45 x as wide as its median length; features of propodeum essentially as described for female. Mesopleurum alutaceous, the upper fovea very small, the lower fovea not at all defined on its upper margin.

Paratypes. — MEXICO: 2 ♂♂, Canyon de Lobos, near Yautepec, Morelos, 4000 feet, 13-18 March 1959 (H. E. Evans) [MCZ, USNM].

Variation. — The two male paratypes are dull black, without any metallic reflections on the head and thorax, and the front is much more strongly alutaceous and less shining. LFW is 2.5 and 2.7 mm; WH is 1.03 and 1.08 x LH, WF 1.23 and 1.25 x HE, OOL 1.17 and 1.20 x WOT. The propodeum is very similar to that of the allotype both in shape and in sculpture, and the mesopleura are also very similar.

13. Rhabdepyris (Trichotepyris) fortunatus new species

Holotype. — ♀, COSTA RICA: Alajuela Prov., Banks of Rio Fortuna, near La Fortuna, Canton San Carlos, 17 February 1964 (sweeping low vegetation in pasture; H. E. Evans) [MCZ, No. 30,943].

Description of female type. — Length 3.7 mm; LFW 2.4 mm. Head and thorax black; abdomen black except apical two segments wholly rufo-testaceous; palpi straw-colored; mandibles testaceous; antennae rufo-testaceous beneath, segments two and three wholly of this color, scape and segments 4-13 dark brownish above; tegulae testaceous; coxae and femora dark brown, hind tibiae somewhat infuscated, legs otherwise light castaneous; wings subhyaline, veins and stigma light brown. Mandibles with five teeth (Fig. 45). Clypeus forming a distinct angle which is only slightly greater than a right angle; median carina nearly straight in profile. WH 1.03 x LH; front moderately wide, WF .66 x WH, 1.28 x HE; OOL 1.23 x WOT. Scrobes not carinate; vertex very broadly rounded off a short distance above the eye tops. Front strongly shining, weakly alutaceous, with small punctures which are fairly close below but very widely spaced toward the vertex. First four antennal segments in a ratio of about 25:7:5:8, segment three unusually short, only about .7 x as long as wide, segment four about 1.2 x as long as wide, segment eleven barely longer than wide. (Fig. 9.)

Thoracic dorsum slightly more evidently alutaceous than the front, with small, well-spaced punctures. Posterior margin of pronotum not paralleled by a groove. Mesoscutum weakly transversly impressed; notauli diverging and attenuate anteriorly; scutellar groove fairly strong, deflected backward and slightly widened on each side. Propodeal disc 1.3 x as wide as long, with five discal carinae, transversely ridged between the carinae, the space between the lateral discals and the lateral carinae polished and with only weak surface sculpturing; side-pieces shining, somewhat alutaceous, with a tendency toward the formation of fine longitudinal striae. Mesopleurum shining, weakly alutaceous; upper fovea ovoid; lower fovea with its upper margin broadly obsolete. Front femora 2.1 x as long as wide; middle tibiae weakly spinose.

Remarks. — This species closely resembles the preceding in head shape and in most standard measurements. The legs are darker in color, and the third antennal segment much shorter; there are also differences in the sculpturing of the pronotum and propodeum and in the shape of the scutellar groove. The species is known only from the type.

14. Rhabdepyris (Trichotepyris) lupus new species

Holotype. — ♂, MEXICO: Canyon de Lobos, near Yautepec, Morelos, 4000 feet, 13 April 1959 (H. E. Evans) [MCZ, No. 30,944].

Description of male type. — Length 4.6 mm; LFW 3.4 mm. Black, the head and thoracic dorsum with very faint, dark olive-green reflections in certain lights, the apical abdominal segment suffused with light brown; palpi and tegulae testaceous; mandibles rufo-testaceous on the apical half, black basally; first three antennal segments bright, pale castaneous (except scape weakly infuscated above), segment four and beyond dark brown, slightly paler below than above; legs bright rufo-testaceous except all coxae blackish, the tarsi quite pale; wings subhyaline, veins and stigma brownish. Clypeus rounded apically, with a small median angulation formed by the end of the strong, arched median carina. WH 1.01 x LH; WF .62 x WH, 1.16 x HE; ocellar triangle compact, front angle much less than a right angle; OOL 1.23 x WOT. Antennal scrobes rather sharply margined above, but not actually carinate; vertex passing straight across a rather short distance above the eye tops. Front moderately shining although strongly alutaceous, actually beaded on the lower part, the punctures obscure. First four antennal segments in a ratio of about 28:7:4:23, segment four 2.4 x as long as wide, segment eleven 2.6 x as long as wide.

Thoracic dorsum more shining and less strongly alutaceous than the front, also with distinct small punctures; posterior margin of pronotum paralleled by a distinct foveolate groove; notauli slender throughout, diverging anteriorly; scutellar groove rather broad, expanded on each side. Propodeal disc measuring 1.33 x as wide as its median length, with seven longitudinal carinae, the surface with fine, oblique striae except smooth and polished near the posterior margin; declivity with transverse striae, side-pieces with fine longitudinal striae. Mesopleurum moderately alutaceous, the lower fovea well defined below and at both ends, but the upper margin broadly discontinuous.

Remarks. — This species is known from the type only. It is distinctive by virtue of the narrow, beaded front and the brightly colored legs.

15. RHABDEPYRIS (TRICHOTEPYRIS) CAROLINIANUS new species

Holotype. — ♀, SOUTH CAROLINA: Florence, 18 January 1938 (no collector given) [MCZ, No. 30,945].

Description of female type. — Length 6.0 mm; LFW 3.3 mm. Head dark olive-green, thoracic dorsum also of this color but the pronotum with faint coppery reflections, the pleura nearly black; propodeum black; abdomen piceous, except suffused with reddish brown on the apical third; palpi testaceous; mandibles ferruginous; antennae light castaneous except upper surface of flagellum slightly infuscated on the outer two-thirds; tegulae testaceous; legs light castaneous except the front coxae strongly infuscated; wings very lightly tinged with brownish, more especially around the radial vein of the fore wing. Body with abundant whitish to pale golden, short setae. Mandibles with five teeth, the basal three teeth broad and blunt (Fig. 46). Clypeus short, broadly rounded except with a faint median angulation; median carina very strongly arched in profile. Head .98 x as wide as high; front narrow, WF .60 x WH, 1.10 x HE; OOL 1.35 x WOT; front angle of ocellar triangle less than a right angle. Vertex passing straight across a distance above eye tops equal to less than half HE; antennal scrobes not carinate. Front alutaceous, moderately shining, strongly punctate, the punctures separated by 1-2 x their own diameters. First four antennal segments in a ratio of about 17:5:4:6, segment three barely longer than its maximum width. (Fig. 7.)

Pronotal disc rounded anteriorly and laterally, about twice as long along the midline as the mesoscutum, its surface alutaceous, moderately shining, with strong punctures which are separated by 2-3 x their own diameters, posterior margin paralleled by a weak, obscurely punctate depression. Mesoscutum not transversely depressed; notauli diverging anteriorly, of uniform width throughout; mesoscutum and scutellum alutaceous, punctate throughout, the punctures slightly smaller than those on the pronotum; scutellar groove strong, deflected backward on each side. Propodeal disc 1.25 x as wide as long; disc with a large, basal, median area filled with longitudinal carinae connected by cross-carinae; there are five strong longitudinal carinae, with four additional, somewhat weaker and more irregular carinae between them, such that nine carinae can be readily counted; disc somewhat shining, weakly transversely striolate on the sides behind; side-pieces longitudinally striolate. Mesopleurum with both upper and lower fovea completely formed, the lower fovea elongate and only weakly constricted near the middle (Fig. 28). Front femora 2.4 x as long as wide; middle tibiae weakly spinose.

Paratype. — ♀, FLORIDA: Gainesville, 5 September 1958 (K. W. Cooper) [USNM].

Variation. — The paratype is smaller (about 5 mm, LFW 2.9 mm) and is similarly colored except as follows: front with faint coppery reflections, but thorax without such reflections; antennae and legs (except front coxae) darker than in the type, more or less ferruginous. WH/LH is 1.0; WF is .63 x WH, 1.13 x HE. Otherwise the resemblance to the type is very close.

Remarks. — I have seen no males which might belong to this species.

16. RHABDEPYRIS (TRICHOTEPYRIS) SUBAENEUS Kieffer

Rhabdepyris subaeneus Kieffer, 1906, Berlin. Ent. Zeitschr., 50: 248 [Type: ♀, NICARAGUA: San Marcos (Coll. C. F. Baker) (Pomona College, Claremont, Calif.)].

Rhabdepyris (Trichotepyris) subaeneus Kieffer, 1908, Genera Insect., 76: 32.

Rhabdepyris (Rhabdepyris) subaeneus Kieffer, 1914, Das Tierreich, 41: 358.

Description of female type. — Length 4.5 mm; LFW 2.9 mm. Head and thorax black, with a very weak metallic green luster; propodeum black; abdomen shining black, apical two segments and sting-palps suffused with rufous; mandibles wholly rufo-castaneous; antennae uniformly castaneous; tegulae testaceous; coxae black, dark brown blotches on the outer side of the front and hind femora, legs otherwise bright yellowish brown; wings hyaline. Mandibles fairly broad, with five teeth in an oblique series, basal three teeth somewhat rounded, the basal tooth wider than third and fourth teeth (Fig. 47). Clypeus obtusely subangulate apically, with a high median carina which is arched in profile. First four antennal segments in a ratio of about 35:9:9:11, segment three 1.1 x as long as thick, segment eleven 1.2 x as long as thick. Antennae arising well below bottoms of eyes; scrobes not margined by carinae. Front shining, uniformly but rather weakly alutaceous, punctures strong, separated by about or slightly more than their own diameters. Head higher than wide, WH 0.92 x LH; front narrow, WF .59 x WH, .95 x HE; distance from eye tops to vertex crest equal to only about .3 x HE. Ocelli small, well separated, front angle of ocellar triangle less than a right angle; OOL 1.2 x WOT; front ocellus below a line drawn between eye tops, posterior ocelli separated from vertex crest by about twice their own diameters. Pronotum with disc separated from collar by a short, oblique anterior face; disc with fairly sharp margins in front and on the sides, but without carinae, also without a groove paralleling the posterior margin (merely with a barely depressed line of punctures); disc somewhat shining, alutaceous, punctures somewhat weaker and more widely spaced than on the front. Mesoscutum strongly alutaceous, rather weakly shining, punctures small but numerous on posterior half; notauli slender, strongly diverging anteriorly, absent on anterior third. Scutellar disc wholly alutaceous, moderately shining; basal groove fairly broad, somewhat turned backward on sides. Propodeal disc 1.25 x as wide as long, with strong lateral and posterior carinae; disc with seven carinae, but the two carinae closely paralleling the median carina rather weak, only the median carina reaching the posterior margin; disc otherwise transversely striate, the striations obsolescent postero-laterally, where the disc is smooth and polished. Mesopleurum with upper and lower foveae distinct, the latter not divided although somewhat constricted near the middle. Front femora 2.1 x as long as wide.

Remarks. — I have seen no specimens of this species other than the type.

17. RHABDEPYRIS (TRICHOTEPYRIS) ANGUSTICEPS new species

Holotype. — ♀, ARIZONA: Tucson, 18 June 1938 (R. H. Crandall) [MCZ, No. 30,946].

Description of female type. — Length 5 mm; LFW 3 mm. Black, except as follows: pronotal collar rufo-testaceous; abdomen suffused with reddish brown on the apical third, the last tergite pale castaneous; palpi straw-colored; mandibles ferruginous; antennae light rufo-castaneous; tegulae testaceous; legs light castaneous except all coxae blackish, front and hind femora partially suffused with black on their outer faces; wings subhyaline, weakly suffused with brown around the radial vein of the fore wing, the veins and stigma amber. Mandibles large, their lower margin weakly arched, the five teeth in a strongly oblique series, the basal three teeth very broad and blunt (Fig. 48). Clypeus very short, very broadly, obtusely angulate, the median carina arched in profile. Head unusually elongate.

.91 x as wide as high; WF .66 x WH, 1.28 x HE; ocelli small, front angle of ocellar triangle less than a right angle, OOL 1.75 x WOT. Sides of head gradually convergent behind the eyes, the vertex relatively narrow, very weakly concave in anterior view; distance from eye tops to vertex crest equal to about .7 x HE. Antennal scrobes not carinate. Front strongly shining, very weakly alutaceous, with strong punctures which are separated by 1.5-3 x their own diameters. Scape flattened, curved; first four antennal segments in a ratio of about 4:1:1:1; segment three 1.3 x as long as its maximum width. (Fig. 8.)

Pronotal disc abruptly rounded anteriorly and on the sides, along the midline 2.4 x as long as the mesoscutum; pro- and mesonota more strongly alutaceous than front, moderately shining, with small, rather evenly distributed punctures; posterior margin of pronotum not paralleled by a punctate groove. Mesoscutum not depressed; notauli linear, strongly diverging toward the front; scutellar groove of moderate breadth, deflected backward on each side. Propodeal disc 1.15 x as wide as long; disc with seven longitudinal carinae, the two carinae close beside the median carina somewhat weaker than the others; surface weakly transversely striolate except on the posterior part; sublateral carinae absent; side-pieces strongly longitudinally striolate. Mesopleurum moderately alutaceous; upper fovea complete; lower fovea elongate, its upper margin obsolete for much of its length. Front femora broad and flat, measuring 1.9 x as long as wide; middle tibiae with a series of small spines on the upper surface.

Remarks. — The tips of all the tarsi of the type and only known specimen are missing.

18. RHABDEPYRIS (TRICHOTEPYRIS) OLIVACEUS new species

Holotype. — ♂, PANAMA: Barro Colorado Island, Canal Zone, 28 March 1955 (C. W. Rettenmeyer) [USNM, No. 67,539].

Description of male type. — Length 3.7 mm; LFW 2.5 mm. Head and thorax black, the front and thoracic dorsum with olive-green reflections; abdomen dark brown, shining, slightly paler toward the base and apex; palpi and tegulae testaceous; mandibles testaceous except blackish toward the base, the teeth rufous; antennae dark brown, the scape partially suffused with black, the flagellum paler beneath than above, antennal segments 2 and 3 tending to be slightly paler than the others; legs testaceous except the front coxae rather strongly infuscated, the femora and the remaining coxae suffused with brownish; wings subhyaline, veins and stigma light brown. Median lobe of clypeus prominent, obtusely angulate except the median point drawn out to an acute angle; median ridge high and arched. WH/LH = 1.0; WF .62 x WH, 1.14 x HE; ocellar triangle compact, front angle less than a right angle; OOL 1.16 x WOT. Antennal scrobes margined by a rounded, ill-defined carina which does not nearly reach the eye margins; vertex elevated only slightly above the eye tops. Front uniformly and rather strongly beaded, somewhat shining, punctures obscure. First four antennal segments in a ratio of about 20:5:3:15, segment four 2.5 x as long as wide, segment eleven twice as long as wide.

Pronotal disc beaded like the front, quite sharply margined on the sides, the posterior margin paralleled by a row of fairly strong foveae. Mesoscutum obscurely punctate, strongly alutaceous, the notauli arching, divergent toward the front; scutellar groove relatively broad, roundly expanded and deflected backward on each end. Propodeal disc measuring 1.15 x as wide as long; disc with five carinae, between which it is irregularly transversely ridged, outside the carinae wholly covered with fine transverse striations; declivity and side pieces covered with rather weak, irregular striations. Mesopleurum somewhat alutaceous although strongly shining, the upper margin of the lower fovea not at all defined. Claws strongly dentate.

Paratypes. — PANAMA: 1 ♂, same data as type except 11 February 1955 [KU]. COLOMBIA: 1 ♂, La Cumbre, 6000 feet, 23 May 1914 (H. S. Parish) [MCZ].

Variation. — The Panama paratype resembles the type closely in every respect. The Colombia paratype is very slightly larger (LFW 2.7 mm) and has the abdomen wholly castaneous, contrasting to the head and thorax, and the front is more shining and with a faint bluish cast (the pronotum, however, is olive-green). In this specimen WF is 1.25 x HE, OOL 1.40 x WOT. In every other respect the resemblance to the type is so close that there seems little question of their conspecificity.

19. RHABDEPYRIS (TRICHOTEPYRIS) PLAUMANNI new species

Holotype. — ♀, BRAZIL: Nova Teutonia, Santa Catarina, 7 July 1937 (F. Plaumann) [BMNH].

Description of female type. — Length 3.7 mm; LFW 2.2 mm.

Head and thorax black, except pronotal collar dark ferruginous: abdomen piceous, except the venter and apical two tergites dark reddish brown; palpi testaceous; mandibles rufo-testaceous, somewhat infuscated toward the base; antennae light castaneous except scape and apical few segments somewhat infuscated; coxae and femora dark brown, hind tibiae medium brown, legs otherwise testaceous; fore wings lightly tinged with brownish, veins and stigma light brown. Mandibles with five teeth, the basal three teeth small and rather blunt. Clypeus short and rather rounded apically, but with a small median angulation formed by the end of the high, arched median carina. Head very slightly wider than high, WH 1.02 x LH; WF .60 x WH, 1.10 x HE; OOL 1.20 x WOT. Antennae arising well below bottoms of eyes, the scrobes not carinate; vertex broadly rounded off a very short distance above the eye tops. Front shining, weakly alutaceous, strongly punctate, the punctures for the most part separated by 1-2 x their own diameters. Antennae rather short, the first four segments in a ratio of about 20:7:5:6, segment three slightly wider than long, segments four through twelve each about as long as thick.

Pronotal disc rather abruptly rounded anteriorly and laterally, measuring along the midline about 1.6 x the length of the mesoscutum; surface alutaceous, moderately shining, punctate; posterior margin paralleled by only a very weak groove. Mesoscutum alutaceous and with small punctures, the notauli slightly attenuated and diverging toward the front; scutellar groove deep but quite thin in the middle, much expanded on each side. Propodeal disc 1.2 x as wide as its median length; disc with 7 carinae, between which it is irregularly transversely ridged; disc laterad of the carina with fine striations which extend to the sublateral carinae; declivity with transverse striae and a median carina; side pieces with longitudinal striations on the basal two-thirds, apically merely alutaceous. Mesopleurum moderately shining and with shallow punctures, the lower fovea not closed above. Front femora 2.3 x as long as wide; middle tibiae not spinose.

Allotype. — ♂, BRAZIL: same data except 29 December 1938 [BMNH].

Description of male allotype. — Length 3.6 mm; LFW 2.3 mm. Head and thorax black, abdomen dark reddish brown; palpi testaceous; mandibles rufo-testaceous apically and on the upper margin, elsewhere blackish; scape black, flagellum dark brown;

coxae and femora dark brown, middle and hind tibiae weakly suffused with brown, legs otherwise testaceous; wings subhyaline. Clypeus forming a distinct angle medially, the angulation slightly greater than a right angle except at the mid-point, where it is acute; median carina very high, strongly arched. WH .98 x LH; WF .63 x WH, 1.22 x HE; ocelli in a compact triangle, OOL 1.15 x WOT. Antennal scrobes not carinate; vertex evenly rounded off a short distance above the eye tops. Front uniformly and rather strongly alutaceous, although somewhat shining, punctures small and shallow, separated by 2-3 x their own diameters. First four antennal segments in a ratio of about 19:6:3:15, segment four 2.5 x as long as wide, segment eleven 2.4 x as long as wide.

Thoracic dorsum uniformly alutaceous, moderately shining, obscurely punctate; pronotal disc rather abruptly rounded on front and sides, its posterior margin paralleled by a strong, foveolate groove; scutellar groove as described for female. Propodeal disc measuring 1.15 x as wide as its median length, with five discal carinae, otherwise wholly covered with fine transverse ridges; side pieces longitudinally striate. Mesopleurum somewhat alutaceous, obscurely punctate, the lower fovea completely open above.

Paratype. — 1 ♂, BRAZIL: same data as type except June 1962 [MCZ].

Variation. — The paratype is only 3.0 mm long, LFW 2.0 mm. The mandibles and legs are somewhat darker than in the allotype, but there are no noteworthy differences in structure. WF is 1.18 x HE, OOL 1.30 x WOT, the propodeal disc 1.2 x as wide as long.

PULCHRIPENNIS SPECIES-GROUP

This group includes four specialized members of this subgenus, all of them small, slender species exhibiting more or less unusual color patterns (at least in the females). The wings are conspicuously banded or, in one species, much abbreviated. The middle tibiae are weakly if at all spinose, the eyes relatively large and very densely hairy.

20. RHABDEPYRIS (TRICHOTEPYRIS) PULCHRIPENNIS new species

Holotype. — ♀, COSTA RICA: Turrialba, 24 June 1949 (K. W. Cooper) [USNM, No. 67,540].

Description of female type. — Length 3.7 mm; LFW 2.6 mm. Head and thorax black, with extremely faint coppery reflections, the pronotal collar ferruginous; propodeum and abdomen shining black, the tip of the abdomen suffused with reddish brown; palpi and mandibles testaceous, the antennae also of this color except the apical segment tipped with fuscous; tegulae testaceous; legs bright testaceous except the front and middle femora weakly and in part suffused with fuscous; wings subhyaline except the fore wing with a fuscous cloud over the outer half of the median and submedian cells and a second fuscous cloud in and below the marginal cell; veins brown except yellowish at extreme base of wing. Body with fairly dense, short, golden brown setae. Mandibles with five teeth, the basal three teeth small and sharp. Clypeus sharply, obtusely angulate. Head 1.03 x as wide as high; front narrow, WF .62 x WH, 1.08 x HE; OOL 1.45 x WOT. Front alutaceous, rather weakly shining, with small punctures which are separated, for the most part, by 1.5-2.5 x their own diameters. Vertex rounded off a short distance above the eye tops; antennal scrobes not carinate. First four antennal segments in a ratio of about 11: 3:2:3, segment three considerably wider than long.

Pronotal disc 1.5 x as long medially as mesoscutum, alutaceous and punctate much like the front, without a line of punctures paralleling the posterior margin. Notauli diverging and attenuated anteriorly; mesoscutum weakly depressed laterad of notauli. Scutellar groove turned backward and considerably widened on each side. Propodeal disc 1.05 x as wide as long; disc with five strong carinae, the median carina complete and the others nearly so, transversely ridged between the carinae; posterior lateral part of disc smooth and polished; side-pieces not striolate, merely weakly aciculate. Mesopleurum with the foveae incompletely defined. Front femora 2.0 x as long as wide; middle tibiae spinose.

Remarks. — This species is known only from the type.

21. Rhabdepyris (Trichotepyris) iridescens new species

Holotype. — ♀, MEXICO: 4 mi. E Cuernavaca, Morelos, 6000 feet, 25 June 1959 (H. E. Evans) [MCZ, No. 30,949].

Description of female type. — Length 3.6 mm; LFW 2.6 mm. Head black, front with strong violet reflections; thorax black, the dorsum with coppery reflections, the pronotal collar ferruginous; propodeum and abdomen shining black, the extreme tip of the abdomen dull brownish; palpi and mandibles testaceous, antennae of this color but the outer side of the flagellum somewhat darker, the apical five segments distinctly infuscated; tegulae testaceous; legs wholly bright rufo-testaceous; wings hyaline except the fore wing with a fuscous cloud over the outer half of the median and submedian cells and a second cloud around and below the radial vein; wing veins brown where the membrane is clouded, elsewhere (including the stigma) testaceous. Mandibles with five teeth, the basal three teeth short and rounded. Clypeus obtusely angulate. Head .92 x as wide as high; front very narrow, WF .59 x WH, .93 x HE; OOL 1.40 x WOT. Front strongly alutaceous although somewhat shining, punctures very shallow and inconspicuous. Vertex rounded off a short distance above eye tops; antennal scrobes not carinate. First four antennal segments in a ratio of about 14:4:4:5, segment three slightly longer than wide. (Fig. 10.)

Pronotal disc 1.2 x as long medially as the mesoscutum, alutaceous and obscurely punctate like the front, with a line of small foveae paralleling the posterior margin. Notauli linear, arcuately diverging anteriorly; mesoscutum not notably depressed on the sides. Scutellar groove slightly broadened and deflected backward on each side. Propodeal disc 1.1 x as wide as long; disc with seven strong carinae, finely transversely striate throughout, but the striae obsolescent on the sides behind; sublateral carina not distinct; posterior angles foveolate; side-pieces shining, weakly aciculate. Mesopleurum with the foveae incompletely defined. Front femora 2.3 x as long as wide; middle tibiae only very weakly spinose.

Remarks. — This remarkably colored species is known only from the type, which was collected at honeydew on the foliage of walnut trees.

22. RHABDEPYRIS (TRICHOTEPYRIS) CUPREOLUS new species

Holotype. — ♀, BRAZIL: Nova Teutonia, Santa Catarina, July 1953 (F. Plaumann) [MCZ, No. 30,950].

Description of female type. — Length 3.8 mm; LFW 2.4 mm. Head and thorax black, the front with coppery reflections, the thoracic dorsum with obscure coppery to olive-green reflections, the pronotal collar ferruginous; propodeum black; abdomen piceous, suffused with light brown toward the apex, the last segment testaceous; palpi straw-colored; mandibles rufo-testaceous, slightly darker on the apical half than basally; antennae wholly testaceous except all segments weakly infuscated on the upper side; tegulae testaceous; legs bright testaceous except front coxae mostly fuscous, front femora partially infuscated on the outer surface; wings faintly luteous, fore wing with two broad fuscous bands separated by a narrow sub-hyaline band which includes the stigma, as in the preceding two species. Mandibles with five teeth, the basal three teeth rather small. Clypeus broadly, obtusely subangulate, the median ridge arched in profile. Head .93 x as wide as high; front very narrow, WF .57 x WH, .95 x HE; ocelli in a compact triangle, OOL 1.25 x WOT. Antennal scrobes not carinate; vertex rounded off a short distance above the eye tops. Front strongly alutaceous, rather weakly shining, with shallow punctures which are separated by 1-3 x their own diameters. First four antennal segments in a ratio of about 27:8:6:9, segments three and eleven barely longer than wide, segment four about 1.3 x as long as wide.

Thoracic dorsum strongly alutaceous, weakly shining, the punctures obscure; pronotum with a strong foveolate groove paralleling the posterior margin; notauli linear, diverging anteriorly; scutellar groove rather wide, roundly expanded at each end. Propodeal disc 1.05 x as wide as long; disc with five longitudinal carinae and with two additional weak carinae close beside the median carinae, otherwise wholly covered with transverse striae; side-pieces wholly covered with fine longitudinal striae which tend to curve upward posteriorly. Mesopleurum strongly alutaceous, the lower fovea elongate, fairly well defined. Front femora slender, 2.4 x as long as wide; middle tibiae not spinose.

Paratypes. — BRAZIL: 1 ♀, same data as type [Coll. G. R. Ferguson]; 1 ♀, Bocaiuva, Parana, 1000 meters elev., May 1963 (F. Plaumann) [MCZ].

Variation. — The topotypic paratype is of the same size as the type, but differs slightly in color: the coppery reflections of the front and pronotum are rather strong, and the front also has rather strong violet reflections, especially anteriorly; the front coxae are only slightly infuscated, and the front femora are wholly without infuscation. In this specimen WH/LH is .94, WF/HE is .96, and OOL/WOT is 1.35. The Bocaiuva paratype is larger (LFW 2.9 mm) but colored like the type. In this specimen WH/LH is .92, WF/HE is .88, and OOL/WOT is 1.33.

23. RHABDEPYRIS (TRICHOTEPYRIS) AMABILIS Fouts

Rhabdepyris amabilis Fouts, 1927, Proc. Ent. Soc. Washington, 29: 165-166 [Type: ♀, MARYLAND: Glen Echo, July (R. M. Fouts) (Coll. Fouts)]. —Muesebeck and Walkley, 1951, U.S. Dept. Agri., Monogr. 2, p. 729.

Description of female type.—Length 3.5 mm; wings very short, fore wing reaching slightly past the middle of the propodeum, LFW 0.55 mm. Head and thorax black, faintly aeneous, except the pronotal collar testaceous; propodeum black; abdomen piceous, fading to dark brown apically; palpi light brown; mandibles and basal three antennal segments pale castaneous, rest of antenna dull castaneous below, dark brownish above; tegulae testaceous; legs bright, pale castaneous except front coxae moderately infuscated; wings hyaline, the veins testaceous. Body clothed with short, golden setae. Mandibles with five teeth, the basal three teeth subequal except the basal tooth more rounded than the others. Clypeus with its median lobe moderately prominent, rounded, with a strong median carina which is arched in profile. Head relatively long and slender, only 1.2 x as wide as maximum width of thorax (across mesothorax); WH .93 x LH; WF .60 x WH, 1.05 x HE; ocelli small, front angle of ocellar triangle less than a right angle; OOL 1.80 x WOT. Antennal scrobes not carinate; temples not well developed; vertex rounded off a distance above eye tops equal to slightly more than half HE. Front alutaceous, moderately shining, punctures moderately strong, small, separated by 2-3 x their own diameters. First four antennal segments in a ratio of about 31:7:7:9, segment three about as long as its apical width.

Pronotum quite long, the disc nearly 3 x the length of the mesoscutum, the punctures small, more widely spaced than on the front; posterior margin paralleled by only a very faint, non-foveolate groove. Mesoscutum short, transversely depressed, especially laterally, the surface rather strongly alutaceous, obscurely punctate; notauli slender, diverging anteriorly; scutellar groove moderately wide, deflected backward but not enlarged on each end. Propodeal disc about as long as wide, the median carina complete, paralleled by two other incomplete carinae, the surface reticulate between and beside these carinae and tending to form two additional weak carinae close beside the median carina; elsewhere smooth, weakly alutaceous, with a few weak longitudinal striae at the extreme upper basal angles. Mesopleurum rather irregularly pitted, the lower fovea not defined on its upper side. Front femora 2.3 x as long as wide; middle tibiae not spinose above. Fore wings slender, nearly 4 x as long as wide, with three longitudinal veins which unite apically to form two cells; hind wings even more slender, reaching to about the apex of the cells of the fore wings.

Plesiallotype. — ♂, VIRGINIA: Falls Church, 2 August (N. Banks) [MCZ].

Description of male plesiallotype. — Length 3.4 mm; LFW 2.3 mm. Head and thorax piceous, abdomen dark reddish brown, paler at base and apex; palpi straw-colored; mandibles rufo-testaceous, darker basally; antennae uniformly medium brown except the second segment slightly paler, the scape weakly infuscated above; tegulae light brown; coxae and femora dark brown, tibiae medium brown, trochanters and tarsi light brown; wings hyaline, veins and stigma light brown. Clypeus with a prominent median lobe which is somewhat rounded but with a median tooth, which is at the end of the high, arched median carina. WH/LH = 1.0; WF .64 x WH, 1.35 x HE; ocelli in a small triangle, the front angle less than a right angle, OOL 1.45 x WOT. Antennal scrobes not carinate; vertex broadly rounded off a distance above eye tops equal to about half HE. Front somewhat shining although very strongly alutaceous, more or less beaded, obscurely punctate. First four antennal segments in a ratio of about 21:6:5:15, segment four 2.5 x as long as wide, segment eleven 3 x as long as thick.

Pronotal disc about 1.2 x as long as mesoscutum, measured along midline, its posterior margin paralleled by a series of small but well defined foveae, the disc otherwise obscurely punctate, alutaceous but by no means beaded like the front. Surface of mesoscutum about like that of the pronotum, the notauli linear, diverging toward the front; scutellar groove arching backward on the sides, wider laterally than medially. Propodeal disc 1.35 x as wide as long; disc with five carinae, the most lateral ones rather short; surface reticulate between the carinae, elsewhere finely transversely striolate, the striae obsolescent posteriorly; declivity with transverse striae and an incomplete median carina; side-pieces alutaceous, with fine longitudinal striae toward the front. Mesopleurum alutaceous, obscurely punctate, the upper margin of the lower fovea not well defined.

Specimens examined. — MASSACHUSETTS: 1 ♀, Lexington, 28 August 1955 (mesic forest, W. L. Brown) [MCZ]. MARYLAND: 1 ♀, Glen Echo [type, coll. Fouts]. DISTRICT

OF COLUMBIA: 1 ♀, Washington, September (J. C. Bridwell) [USNM]. VIRGINIA: 1 ♀, 3 ♂♂, Falls Church, 2-11 August (N. Banks) [MCZ]. FLORIDA: 2 ♀♀, Gainesville, May, October 1958, 1959 (K. W. Cooper) [USNM].

Variation. — The three males vary slightly in size (LFW 2.2-2.5 mm) and show some variation in the degree of infuscation of the legs and antennae. In the two specimens other than the plesiallotype the lateral ocelli are somewhat less far removed from the eyes, OOL being 1.25 x WOT in both specimens. WF varies from 1.30 to 1.35 x HE; the propodeal disc varies from 1.2 to 1.35 x as wide as long.

The available females show so much variation that one is tempted to place them in several subspecies. However, since only six specimens are at hand, and since some of the variation appears allometric (e.g. relatively longer wings in the larger specimens) and much of it clinal (e.g. brighter colors and narrower front toward the south), it would be premature to erect subspecies at this time. Some of the variation is tabulated below (Table IV). In spite of this variation, it should be pointed out that the entire series is much alike with respect to form of the mandibles and clypeus and features of the thoracic dorsum and propodeum. The two Florida specimens are strikingly colored, having the head ferruginous except the central part of the front black, the thorax and propodeum ferruginous except the mesoscutum spotted with black laterad of the notauli, and the first two abdominal segments maculated with ferruginous basally.

TABLE IV. VARIATION IN SIX FEMALES OF RHABDEPYRIS AMABILIS FOUTS

Locality	Length (mm.)	Wing length (mm.)	Color of legs	Color head and thorax	WH/LH	WF/HE	OOL/WOT
Massachusetts	3.3	.45	brownish	black, slightly aeneous	.93	1.13	1.75
Maryland	3.5	.55	testaceous	as above	.93	1.05	1.80
Dist. Columbia	4.7	.75	as above	as above	.94	1.05	1.65
Virginia	4.3	.60	as above	as above	.95	1.12	1.70
Florida	3.3	.50	light brown	mostly ferruginous	.97	0.90	1.40
Florida	3.0	.40	as above	as above	.94	0.96	1.55

C. Subgenus CHLOREPYRIS Kieffer

Chlorepyris Kieffer, 1913, Boll. Lab. Zool. Portici, 7: 108 (type species: *C. semiviridis* Kieffer 1913 [= *viridissimus* Kieffer 1911]; designated by Kieffer, 1914). —Kieffer, 1914, Das Tierreich, 41: 412-416 (key to spp., Oriental and Neotropical regions). —Kurian, 1955, Agra Univ. Jour. Res., 4: 101-105 (Oriental spp.).

Subgeneric characters. — Small to fairly large bethylids (up to 10 mm); black, head and thorax often weakly to strongly greenish or bluish, abdomen sometimes in part rufous; eyes glabrous; body clothed with fine, pale setae which are mostly subappressed except more erect and bristling on the abdomen, temples, and propleura; middle tibiae of female spinose, hind tibiae of female and tibiae of male also sometimes spinose. Mandibles of male terminating in five small, sharp teeth, those of female with from three to five apical teeth and also often with a subapical tooth on the lower margin; malar space short, about as in *Trichotepyris;* antennal scrobes not margined in the known American species; third antennal segment of male of very variable length, but always quite distinctly separated from the fourth segment. Pronotum rather long, its posterior margin not paralleled by a foveolate groove; mesoscutum more or less transversely depressed in the females of most species; notauli strong, reaching anterior margin usually only as very fine lines; scutellar groove slender and arcuate or sometimes rather straight and much broadened on each side, in a few species merely forming a thin line connecting large lateral pits; propodeal disc with from three to seven longitudinal carinae, its postero-lateral angles always strongly foveolate. Claws dentate, bifid, or trifid.

Remarks. — As mentioned in the introduction, *Chlorepyris* is here redefined in a somewhat broader sense than Kieffer's. There are three species-groups, of which the third (the *viridissimus* group) more or less approximates *Chlorepyris* in Kieffer's sense.

KEY TO SPECIES OF SUBGENUS *CHLOREPYRIS*

Females

1. Lower mesopleural fovea well defined, fully outlined or with the upper margin indistinct on the middle fourth (Figs. 29, 30); mandibles with the preapical tooth on the lower margin small and inconspicuous (Fig. 49); species of black, non-metallic coloration (*Lobatifrons* group) 2

Lower mesopleural fovea poorly defined, its upper margin completely undefined for at least the middle third (Figs. 31-36); mandibles with a strong, sharp tooth on the lower margin (Figs. 50-54); color variable 4

2. Wings strongly suffused with yellowish; LFW at least 4.5 mm; front broad, WF 1.25-1.50 x HE (Fig. 11); OOL more than 2.0 x WOT; lower mesopleural fovea strongly outlined (Fig. 29) . . . . 24. *luteipennis* n. sp.

Wings somewhat clouded, barely if at all yellowish; LFW 3.0-3.8 mm; OOL less than 2.0 x WOT, sometimes only slightly so; lower mesopleural fovea not always fully defined above (Fig. 30) 3

3. Mandibles mostly pale ferruginous, legs also of this color except femora sometimes darker, coxae fuscous; ocellar triangle fairly broad, front angle only slightly less than a right angle . . . . 27. *quinquelineatus* Kieffer

Mandibles and legs mostly black; front with some strong punctures on the lower part, the punctures smaller and much more widely spaced above; ocellar triangle compact, front angle much less than a right angle (Fig. 12) . . . . 28. *nigerrimus* n. sp.

4. Head well developed in front of eyes, the antennae inserted well below bottoms of eyes (WH less than 1.05 x LH, rarely up to 1.08 x LH) (Figs 13, 14); upper mesopleural fovea small, ovoid, at most about 2.5 x as long as wide (Figs. 31-33); claws dentate (*Muscarius* group) 5

Head very short in front of eyes, antennae arising only slightly below bottoms of eyes, clypeus barely protruding beyond antennal bases (WH at least 1.07 x LH, up to 1.20 x LH (Figs. 15, 16); upper mesopleural fovea elongate, 2-5 x as long as wide (Figs. 34-36); head and thorax with metallic blue or green coloration (*Viridissimus* group) 9

5. Head and thorax black, without metallic colors; scutellar groove very slender, curved backward but barely widened at each end; front femora strongly incrassate 6

Head and thorax weakly to strongly reflecting metallic blue or green; scutellar groove much widened at each end, appearing as a slender line connecting two pits 7

6. Head and thoracic dorsum strongly shining, obscurely alutaceous; upper margin of lower mesopleural fovea defined in front and behind (Fig. 31); OOL 1.40-1.55 x WOT; LFW 3.8-4.2 mm . . . . 29. *muscarius* (Westwood)

Head and thoracic dorsum (especially the latter) moderately shining, quite distinctly alutaceous; upper margin of lower mesopleural fovea not at all defined (Fig. 32); OOL 1.20-1.33 x WOT; LFW 3.2-3.3 mm . . . . 31. *origenus* Kieffer

7. Legs rufous except the coxae black; length about 4 mm; head metallic blue, thoracic dorsum green with bluish reflections . . . . 35. *metallicus* Kieffer

Legs with femora at least partially fuscous and front femora usually with metallic reflections; length 4.5-7.0 mm 8

8. Head and thorax with dull olive-green reflections; propodeal disc 1.25-1.36 x as wide as long; front with very small punctures which are separated by several times their own diameters ....33. *virescens* n. sp.

Head and thorax bright bluish green; propodeal disc only 1.15 x as wide as long; front with strong punctures which are separated by 2-3 x their own diameters ....34. *viridis* (Cameron)

9. Propodeum black, without metallic reflections, contrasting to head and thoracic dorsum, which are greenish 10

Propodeum bluish, blue-green, or violet, either of the same color or contrasting to the thoracic dorsum 11

10. Head and thoracic dorsum with dull olive-green reflections; propodeum elongate, 1.25-1.28 x as wide as long; tooth of claws acute, sloping outwards slightly; LFW 3.0-3.5 mm .... 36. *subviridis* (Kieffer)

Head and thorax intense, brilliant green; propodeum transverse, 1.38-1.45 x as wide as long; tooth of claws somewhat blunt, sloping outward strongly (Fig. 66); LFW 4.0-5.5 mm ....38. *viridissimus* (Kieffer)

11. Legs largely ferruginous except for coxae and hind femora; upper mesopleural fovea only about twice as long as high; propodeum violaceous, contrasting to the brilliant green head and thorax ....39. *fulgens* (Brues)

Legs variable, but the front femora always dark and with strong bluish reflections; upper mesopleural fovea at least 3 x as long as high (Figs. 35, 36); propodeum blue or blue-green, contrasting at most slightly with the head and thoracic dorsum, which are more or less bluish, blue-green, or violaceous 12

12. Legs ferruginous except for the coxae and the front femora; LFW 3.5 mm; front sparsely punctate, mesoscutum with punctures only along the notauli and parapsidal furrows; apical .4 of abdomen ferruginous .... 40. *tricolor* n. sp.

Legs mostly dark, the hind femora black and with bluish reflections like the front femora; LFW 4.5-4.7 mm; front and thoracic dorsum wholly covered with small punctures; tip of abdomen weakly suffused with brownish .... 41. *violaceus* n. sp.

Males

1. Third antennal segment not reduced, distinctly longer than wide, much longer than second segment and nearly or quite as long as fourth (Figs. 71, 72); lower mesopleural fovea fully outlined or the upper margin indistinct on the middle fourth (as in Figs. 29, 30) (*Lobatifrons* group) 2

Third antennal segment small, transverse, wider than long, much shorter than fourth segment (Figs. 19-24, 73); lower mesopleural fovea broadly incomplete above (Figs. 37-42) 5

2. Propodeum with five discal carinae . . . 3
Propodeum with seven discal carinae, five parallel carinae medially and two more oblique carinae laterad of these . . . 4

3. Lower mesopleural fovea fully enclosed (as in Fig. 29); LFW 3.3-4.0 mm; front evidently alutaceous . . . 24. *luteipennis* n. sp.
Lower mesopleural fovea with its upper margin indistinct on the middle third (as in Fig. 30); LFW under 3.0 mm; front strongly polished, at most obscurely alutaceous . . . 27. *quinquelineatus* Kieffer

4. Propodeum very short, transverse, 1.9 x as wide as its median length; tip of abdomen suffused with dull ferruginous . . . 25. *lobatifrons* Kieffer
Propodeum more elongate, measuring 1.6-1.7 x as wide as long; apical third of abdomen bright ferruginous . . . 26. *septemlineatus* Kieffer

5. Upper mesopleural fovea small, completely enclosed (Fig. 37); species of black coloration . . . 6
Upper mesopleural fovea elongate, open behind (Figs. 38-42); black or with metallic colors . . . 7

6. Head very broad (WH 1.12-1.20 x LH) (Fig. 19); front polished and only very obscurely punctate, mesopleura impunctate or nearly so . . . 29. *muscarius* (Westwood)
Head moderately broad (WH 1.07 x LH) (Fig. 20); front with large punctures, mesopleura also punctate . . . 30. *puncticeps* n. sp.

7. Third antennal segment extremely short, about one-third the length of the fourth segment (Fig. 23); head and thorax blue-green, apical .4 of abdomen ferruginous . . . 37. *blantoni* n. sp.
Third antennal segment at least half as long as the fourth (Figs. 24, 73); color variable . . . 8

8. Propodeum black; head and thorax black or various shades of blue or green . . . 9
Propodeum bluish or greenish; head and thorax also metallic, sometimes contrasting slightly with the propodeum; notauli very broad behind . . . 12

9. Head and thorax a very brilliant green or blue-green; claws strongly trifid, the middle ray obliquely truncate (Fig. 67); second antennal segment shorter than third segment (as in Fig. 24) . . . 38. *viridissimus* (Kieffer)
Head and thorax black or weakly to moderately bluish or greenish; middle ray of claws more erect and acute (Figs. 61, 63); second antennal segment longer than third segment (Fig. 21) . . . 10

10. Propodeum short, measuring 1.35-1.46 x as wide as long, generally with a fairly wide smooth area laterad of the lateral discal carinae; front polished, obscurely alutaceous, with weak bluish or greenish reflections . . . 33. *virescens* n. sp.
Propodeum more elongate, 1.25-1.33 x as wide as long, generally almost wholly covered with sculpturing; front somewhat more evidently alutaceous than above . . . 11

11. Head and thorax black and without metallic colors; scutellar groove rather weakly expanded at each end; OOL slightly less than WOT . . . 32. *vesculus* n. sp.

Head and thorax more or less blue-green; scutellar groove much widened on the sides; OOL 1.1-1.25 x WOT, the ocelli being in a more compact triangle than above ....36. *subviridis* (Kieffer)

12. Head and thorax green or blue-green, apical half of the abdomen rufous; notauli separated behind by more than half the width of one notaulus; propodeum with five discal carinae ... .39. *fulgens* (Brues)

Head and thorax intensely bluish or violaceous, abdomen black; notauli unusually wide behind, separated by only a thin line; propodeum with only three well-defined discal carinae ....41. *violaceus* n. sp.

TABLE V. SUMMARY OF SOME CHARACTERS OF TYPE SPECIMENS OF SPECIES OF SUBGENUS CHLOREPYRIS (♀♀)[1]

Species	LFW (mm)	WH/LH	WF/HE	OOL/WOT	Propodeal disc W/L	Front femora L/W	Lower mesopl. fovea fully outlined
24. luteipennis	5.0	0.98	1.47	2.20	1.50	2.1	+
27. quinquelineatus	3.3	1.00	1.17	1.60	1.50	2.4	±
28. nigerrimus	3.8	1.01	1.17	1.90	1.50	2.2	±
29. muscarius	4.0	1.08	1.33	1.50	1.40	1.8	-
31. origenus	3.3	1.08	1.20	1.20	1.40	1.7	-
33. virescens	4.3	1.02	1.30	1.40	1.30	2.0	-
34. viridis	3.0	1.00	1.18	1.40	1.15	1.8	-
36. subviridis	3.5	1.10	1.06	1.60	1.30	2.1	-
38. viridissimus	4.4	1.20	1.10	1.40	1.40	2.2	-
39. fulgens	4.0	1.16	1.23	1.50	1.40	2.0	-
40. tricolor	3 5	1.12	1.18	1.70	1.35	2.0	-
41. violaceus	4 5	1.17	1.20	1.60	1.35	2.4	-

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[1] I have omitted *metallicus* Kieffer, since I have not seen the type or any other specimens. The specimens of *muscarius* and *subviridis* considered are plesiallotypes rather than holotypes; the specimen of *viridissimus* is also a plesiallotype of that species as well as the type of *semiviridis* Kieffer. Five species are not known from the female sex.

TABLE VI. SUMMARY OF SOME CHARACTERS OF TYPE SPECIMENS OF SPECIES OF SUBGENUS CHLOREPYRIS (♂♂)[1]

Species	LFW (mm)	WH/LH	WF/HE	OOL/WOT	Propodeal disc W/L	Antennal seg. three L/W
24. luteipennis	3.5	0.98	1.00	1.55	1.65	1.4
25. lobatifrons	3.6	0.97	0.94	1.50	1.90	1.6
26. septemlineatus	3.4	0.95	1.00	1.35	1.65	1.5
27. quinquelineatus	2.8	1.00	0.90	1.50	1.80	1.3
29. muscarius	3.3	1.12	1.25	1.12	1.60	0.8
30. puncticeps	3.8	1.07	1.36	1.10	1.45	0.6
32. vesculus	2.8	1.10	1.35	0.90	1.30	0.6
33. virescens	3.0	1.08	1.40	1.00	1.40	0.7
36. subviridis	2.8	1.18	1.43	1.10	1.35	0.6
37. blantoni	3.8	1.09	1.10	1.10	1.40	0.3
38. viridissimus	3.6	1.20	1.13	1.05	1.40	0.7
39. fulgens	3.9	1.20	1.24	1.00	1.40	0.7
41. violaceus	3.5	1.18	1.28	0.95	1.30	0.7

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[1] The specimens treated are either holotypes (*lobatifrons*, *septemlineatus*, *muscarius*, *puncticeps*, *vesculus*, *subviridis*, *blantoni*, and *viridissimus*), allotypes (*luteipennis*, *virescens*), or plesiallotypes (*quinquelineatus*, *fulgens*). Five species are not known from the male sex.

Lobatifrons species-group

To this group are assigned five species of black coloration in which the scutellar groove is slender throughout, the head of the females more or less produced in front of the eyes, the lower mesopleural fovea well defined above except margining ridge sometimes obsolescent for a short distance. In the males, the third antennal segment is longer than wide and not notably shorter than the fourth segment; the head of the male is not or barely wider than long, the front narrow, WF not or barely exceeding HE.

24. Rhabdepyris (Chlorepyris) luteipennis new species

Holotype. — ♀, BRAZIL: Nova Teutonia, Santa Catarina, March 1948 (F. Plaumann) [MCZ, No. 30,951].

Description of female type. — Length 8.5 mm; LFW 5.0 mm. Black; palpi light brown; mandibles ferruginous, infuscated below; scape black, flagellum dusky castaneous, darker above than below; tegulae testaceous; coxae black, legs otherwise fusco-ferruginous except paler apically; wings subhyaline, strongly tinged with yellowish except apical third of fore wing smoky, veins and stigma light amber, translucent. Mandibles slender and rather straight, terminating in one strong tooth basad of which are four rather indistinct, blunt teeth (Fig. 49). Clypeus obtusely subangulate, with a median ridge which is nearly straight in profile. WH .98 x LH; sides of head subparallel behind the eyes, the vertex passing straight across a considerable distance above eye tops. Front broad, eyes convergent below; WF .66 x WH, 1.47 x HE; ocelli in a compact triangle far above eyes and close to vertex crest, OOL 2.2 x WOT. Front strongly shining, barely alutaceous, punctures small but sharply defined, separated by 2-4 x their own diameters below, much more widely spaced above. Antennae arising well below bottoms of eyes from beneath prominent lobes; first four segments in a ratio of about 23:5:6:9, segment three slightly wider than long, segment eleven about 1.5 x as long as wide. (Fig. 11.)

Thoracic dorsum shining and obscurely alutaceous like the front, the punctures small and widely spaced; pronotal disc about 2.5 x as long as mesoscutum; notauli attenuated and slightly diverging anteriorly; parapsidal furrows short and rather wide; scutellar groove moderately wide, deflected backward and slightly widened on each side. Propodeal disc 1.5

x as wide as long; disc with five carinae between which it is weakly transversely striate, otherwise smooth and polished; lateral carinae paralleled by a simple groove, but the sublaterals not distinct; declivity smooth except for very fine transverse striations; side-pieces with very delicate longitudinal striae. Mesopleurum polished, with small, sparse punctures; upper fovea small, ovoid; lower fovea elongate, fully outlined, much broadened on the posterior .6 (Fig. 29). Middle tibiae spinose above for their entire length; claws twice-dentate, the middle tooth short, sloping outward (Fig. 55); front femora much broadened, measuring 2.1 x as long as their maximum width.

Allotype. — ♂, BRAZIL: Santarem (no further data) [USNM].

Description of male allotype. — Length 5.0 mm; LFW 3.5 mm. Head and thorax black; abdomen black except segments narrowly brownish apically, last two segments mostly brownish; palpi testaceous; mandibles light rufo-castaneous; antennae wholly and uniformly light castaneous; tegulae testaceous; coxae black, hind femora fuscous, legs otherwise bright rufo-castaneous; wings lightly tinged with yellowish brown, not darkened apically. Clypeus as described for female. WH .98 x LH, the general form and insertion of antennae as in female; WF .54 x WH, subequal to HE; OOL 1.55 x WOT. Front somewhat more evidently alutaceous and slightly more closely punctate than in female. First four antennal segments in a ratio of about 6:2:3:3, segment three about 1.4 x as long as wide, segment eleven about 1.6 x as long as wide. (Fig. 71.)

Thoracic dorsum weakly alutaceous, the pronotum more so than the mesonotum, punctures weak; features of mesonotum as in female. Propodeal disc 1.65 x as wide as long, with five carinae between which it is weakly transversely striate, elsewhere smooth and polished; declivity strongly polished, barely alutaceous; side-pieces with fine longitudinal striations. Mesopleurum weakly alutaceous, with small punctures, the foveae shaped as in the female, the two foveae separated by a broad, flat ridge. Front femora 2.1 x as long as their maximum width; middle tibiae weakly spinose; claws bifid, the inner ray close to the outer ray, obliquely truncate (Fig. 56).

Paratypes. — BRAZIL: 8 ♀♀, same data as type except various dates, September-March, 1952-'62 [MCZ, USNM, BSA, Coll. G. R. Ferguson]; 1 ♀, Urucum, Corumba, 12-19 December

1919 (C. U. Exped.) [CU]; 1 ♂, Santarem [USNM]. TRINIDAD: 1 ♂, St. Augustine, 25 July 1935 (N. A. Weber) [MCZ]. PANAMA: 1 ♀, March 1923 (no further data) [MCZ]; 1 ♂, Barro Colorado Isl., Canal Zone, 14 June 1939 (J. Zetek) [USNM]. NICARAGUA: 1 ♂, San Carlos, 1933 (Wickham Coll.) [USNM].

Variation. — The females vary in size from 7.5 to 9.5 mm, LFW from 4.5-5.5 mm. The Panama and Nicaragua specimens have the legs beyond the coxae bright rufo-ferruginous, the tip of the abdomen also suffused with this color, but they otherwise show no consistent differences from the Brazilian females. In this series WH varies from .97 to 1.00 x LH, WF from 1.25 to 1.50 x HE, OOL from 2.2 to 2.5 x WOT. The sculpturing of the propodeum and mesopleurum shows little variation throughout the series.

The Santarem male paratype is very similar to the allotype in every respect. The Trinidad and Panama males have the legs beyond the coxae and the tip of the abdomen rufo-ferruginous, as in the Central American females. These two specimens also have both the upper and lower mesopleural foveae larger than in the rest of the type series, the ridge between them narrow and round-topped. This appears to be an important difference, and it may be that these two males go with a different, as yet undiscovered, female; however, in all standard measurements they differ scarcely at all from the Santarem males (although both are slightly larger, LFW 3.9-4.0 mm). The Trinidad male is without antennae.

25. RHABDEPYRIS (CHLOREPYRIS) LOBATIFRONS Kieffer

Rhabdepyris lobatifrons Kieffer, 1910, Ann. Soc. Ent. France, 78: 297-298 [Type: ♂ (not ♀ as stated), BRAZIL: Pará (C. F. Baker) (Pomona College)]. —Kieffer, 1914, Das Tierreich, 41: 361.

? *Rhabdepyris obscuripennis* Kieffer, 1910, Ann. Soc. Ent. France, 79: 40 [Type: ♂ (?), BRAZIL: Pará (C. F. Baker) (location unknown)]. —Kieffer, 1914, Das Tierreich, 41: 359.

Description of male type. — Length 5 mm; LFW 3.6 mm. Wholly shining black except tip of abdomen suffused with dull ferruginous; palpi testaceous; mandibles light castaneous, the tips rufous; antennae wholly and uniformly bright castaneous; tegulae testaceous; legs bright testaceous except all coxae strongly infuscated with yellowish brown, veins and stigma light brown. Clypeus obtusely angulate, its median ridge very weakly arched in profile. Head .97 x as wide as high; front rather narrow, WF .51 x WH, .94 x HE; OOL 1.50 x WOT; front angle of ocellar triangle slightly less than a right angle; distance from eye tops to crest of vertex equal to roughly .5 x HE, the vertex straight across; distance from posterior ocelli to vertex crest about equal to width of an ocellus. Front polished, very obscurely alutaceous, punctures small although sharply defined, separated by 1-2 x their own diameters except more widely spaced toward the vertex. Antennae arising from rather prominent tubercles well below bottoms of eyes; first four antennal segments in a ratio of about 12:3:7:7, segments three and four both 1.6 times as long as wide, segment eleven twice as long as wide.

Thoracic dorsum polished and very obscurely punctate, like the front, the punctures fairly strong but widely spaced, absent on the anterior part of the mesoscutum and center of the scutellum; pronotal disc 1.35 x median length of mesoscutum; notauli strong, barely diverging anteriorly, represented on the anterior half of the scutum only by hair-lines; basal scutellar groove thin, deflected backward and considerably widened on each side. Propodeum very short, the disc 1.9 x as wide as its median length; disc with seven carinae, five of them close together, straight, and nearly complete (the median carina complete), the other two spaced more widely to the sides, arching mesad apically and stopping well short of the transverse carina; disc obscurely striate between the carinae, elsewhere smooth and polished; sublateral carinae absent; posterior corners foveolate. Mesopleurum wholly moderately alutaceous, weakly shining; upper fovea small; lower fovea elongate, weakly constricted in the middle, fully outlined above and below. Middle tibiae weakly spinose; claws bifid.

Remarks. — The type of Kieffer's *obscuripennis* is probably lost. Kieffer did not state the sex in his original description, but in 1914 he indicated questionably that it was a male. One notes that the type locality, size, and color are essentially the same in the types of *lobatifrons* and *obscuripennis*, and no striking differences are apparent from Kieffer's descriptions except that the wings of the latter are "d'un brun sombre." The wings are distinctly tinged with yellowish brown in the type of *lobatifrons*, and I question that the other type is very different. In 1914, Kieffer keyed out *obscuripennis* as having spines on the middle tibia, *lobatifrons* as lacking spines, but examination of the type of *lobatifrons* reveals that spines are present. Kieffer stated that *lobatifrons* has 5 parallel carinae on the propodeum; he neglected to mention that there are two additional, more oblique discal carinae. I suggest that *lobatifrons* and *obscuripennis* be regarded as probable synonyms at least until the type of *obscuripennis* is found.

26. RHABDEPYRIS (CHLOREPYRIS) SEPTEMLINEATUS Kieffer

Rhabdepyris septemlineatus Kieffer, 1906, Berlin. Ent. Zeitsch., 50: 250 [Type: ♂, NICARAGUA: Granada (C. F. Baker) (Pomona Coll.)] —Kieffer, 1914, Das Tierreich, 41: 361.

Description of male type.—Length 4.1 mm; LFW 3.4 mm. Head, thorax, and basal three segments of abdomen shining black, apical four segments of abdomen ferruginous; mandibles yellowish brown, darker basally and apically; antennae light ferrugino-castaneous, somewhat infuscated on apical half; tegulae testaceous; coxae black, femora ferrugino-castaneous, legs otherwise light yellowish brown; wings subhyaline, with dark setulae, veins and stigma brown. Clypeus not prominent, its apical margin obtusely subangulate, median carina not arched in profile. WH .95 x LH; WF .56 x WH, subequal to HE; inner orbits converging below; distance from eye tops to vertex crest equal to slightly over half HE, vertex straight across; ocelli in about a right triangle far above eye tops and close to vertex crest; OOL 1.35 x WOT; hind ocelli removed from vertex crest by less than their own diameter. Front strongly polished, weakly alutaceous on lower sides only, punctures small but fairly prominent, on lower front separated by about their own diameters, on upper front and vertex separated by 2 – 4 x their own diameters. First four antennal segments in a ratio of about 25 :7 :14 :14, segment three about 1.5 x as long as thick, segment eleven about 1.7 x as long as thick; pubescence moderately coarse, subappressed, somewhat golden, erect setae short but fairly numerous.

Pronotal disc not sharply differentiated from collar, about 1.3 x as long as mesoscutum, with smooth contours, weakly alutaceous and with distinct, well separated punctures. Mesoscutum strongly polished, scarcely alutaceous, weakly transversely depressed posteriorly; parapsidal furrows very short, occupying the posterior third of the mesoscutum only, notauli weakly diverging anteriorly, attenuate anteriorly, occupying the posterior half of the scutum. Scutellar disc weakly alutaceous, with a few punctures; basal groove narrow, of uniform width throughout but distinctly deflected backward on each side. Propodeal disc quadrate, 1.65 x as wide as long, lateral and transverse posterior carinae very strong; median portion of disc with five closely parallel carinae which are complete or nearly so, also with two additional carinae laterad of these, extending only slightly more than half the length of the disc; disc otherwise polished and with only some very weak sculpturing; side-pieces weakly longitudinally striolate. Mesopleurum weakly alutaceous, with a well-defined, elongate lower fovea which is widely separated from the small upper fovea (much as in *luteipennis*, Fig. 29). Claws bifid, inner ray truncate; middle tibiae with a few spines; front femora 2.1 x as long as their maximum width.

Additional specimen examined. — PANAMA: 1 ♂, Barro Colorado Isl., Canal Zone, 11 February 1955 (C. Rettenmeyer) [KU].

Variation. — The Panama male is slightly larger than the type and has the front and hind femora moderately infuscated, but it is otherwise very similar, the apical .4 of the abdomen being bright ferruginous as in the type. In this specimen WH is .98 x LH, WF .92 x HE, OOL 1.50 x WOT; the lateral pair of discal carinae extend for about .8 the length of the propodeum.

27. RHABDEPYRIS (CHLOREPYRIS) QUINQUELINEATUS Kieffer

Rhabdepyris quinquelineatus Kieffer, 1906, Berlin. Ent. Zeitschr., 50: 249 [Type: ♀, NICARAGUA: Chinandega (C. F. Baker) (Pomona Coll.)]. —Kieffer, 1914, Das Tierreich. 41: 360.

Description of female type. — Length 5 mm; LFW 3.3 mm. Body shining black, without metallic hues, last two abdominal segments weakly suffused with reddish brown; mandibles and antennae rather uniformly reddish brown, antennal tubercles also suffused with this color; tegulae testaceous; coxae black, legs otherwise reddish brown; fore wing weakly clouded, more noticeably so about the radial vein, veins and stigma brown. Mandibles with five teeth, the basal three teeth very small (essentially as figured for *luteipennis*, Fig. 49). Clypeus forming a subangulate median process, its median elevation rather weak. Head about as wide as high; inner orbits convergent below; WF .61 x WH, 1.17 x HE; vertex straight across a short distance above eye tops, distance from eye tops to vertex crest about half HE. Ocelli in a broad triangle close to vertex crest; OOL 1.6 x WOT; posterior ocelli removed from vertex crest by about their own diameters. Front shining, obscurely alutaceous, with strong punctures which are separated by 1-2 x their own diameters (much more widely spaced above). First four antennal segments in a ratio of about 19:5:5:7, segment three only 1.2 x as long as thick, segment eleven 1.4 x as long as thick.

Pronotum large, with even contours, anteriorly not sharply separated from collar, on the median line 1.8 x as long as mesoscutum; pronotum strongly shining and with large, well-separated punctures. Mesoscutum with a shallow transverse impression, shining and almost impunctate; notauli attenuate and diverging anteriorly; scutellar disc rather flat, basal groove narrow, of even width throughout, its ends turned obliquely backward. Propodeal disc 1.5 x as wide as long, its lateral and posterior carinae strong, also with five carinae on the median area, all of them reaching the posterior margin or nearly so; disc weakly transversely striate between the carinae, on the sides smooth and strongly polished. Mesopleurum strongly polished, with scattered small punctures, lower fovea distinct, about as in *septemlineatus*. Claws bifid, inner ray truncate (Fig. 57); front femora 2.4 x as long as wide; middle tibiae spinose.

Plesiallotype.— ♂, EL SALVADOR: San Salvador, 3-4 May 1958 (O. L. Cartwright) [USNM].

Description of male plesiallotype.—Length 3.7 mm; LFW 2.8 mm. Black, apical two abdominal segments suffused with reddish brown; palpi testaceous; mandibles pale castaneous, the teeth rufous; antennae wholly light brown, except suffused with darker brown on upper surface; coxae black, legs otherwise bright rufo-castaneous; wings subhyaline, veins yellowish toward base of wing. Clypeus obtusely angulate, with a low median ridge. Head as wide as high; eyes strongly convergent below, WF only .49 x WH, .90 x HE; OOL 1.50 x WOT. Front strongly shining, barely alutaceous, with small punctures which are close below, widely spaced above. First four antennal segments in a ratio of about 18:6:10:11, segment three 1.3 x as long as wide (Fig. 72), segment eleven twice as long as wide. Thoracic dorsum strongly polished, non-alutaceous, with small punctures; features as in female. Propodeum very short, the disc 1.8 x as wide as long, features as in female. Mesopleurum shining, with a few small punctures; lower fovea elongate, well defined except the upper margin rather indistinct toward the middle. Claws bifid; middle tibiae with a few small spines above; front femora 2.2 x as long as wide.

Additional specimens examined. — MEXICO: 1 ♀, Medellin, Veracruz (C. F. Baker no. 2154) [USNM]; 1 ♂, Progreso, Yucatan, 23 July 1962 (H. E. Evans) [MCZ].

Variation. — In both of the Mexican specimens, the upper margin of the lower mesopleural fovea is indistinct in the middle. The female differs from the type also in having the third antennal segment slightly wider than long and the femora dark brown, contrasting to the light brown tibiae and tarsi. The Yucatan male also has dark brown femora, but the antennae are lighter than in the plesiallotype; in this specimen the propodeum is also 1.6 x as wide as long.

28. RHABDEPYRIS (CHLOREPYRIS) NIGERRIMUS new species

Holotype. — ♀, BOLIVIA: Santa Cruz, Santiago, November 1959 (no collector given) [KU].

Description of female type. — Length 6.5 mm; LFW 3.8 mm. Wholly black, shining, the apical abdominal tergite suffused with dark brown; palpi brown; mandibles black, flagellum dark brown above, light brown below; tegulae brownish fuscous; legs black except apices of femora and tibae suffused with dark ferruginous, tibial spines and spurs light ferruginous, tarsi castaneous; wings hyaline except fore wing lightly clouded along major veins and on apical .6, more especially around the radial vein, veins and stigma dark brown except veins yellowish at extreme base of wing. Mandibles with a large apical tooth and four small, blunt teeth in an oblique series basad of this, with a small tooth on the lower margin (differing in no important way from those of *luteipennis*, Fig. 49). Clypeus broadly angulate, its median ridge not arched in profile. WH 1.01 x LH; eyes convergent below, WF .61 x WH, 1.17 x HE; front angle of ocellar triangle less than a right angle, OOL 1.9 x WOT. Distance from eye tops to vertex crest about .5 x HE; vertex nearly straight across. Front polished, very obscurely alutaceous; lower part of front with a median streak and with some large, well-spaced punctures, but the punctures on the upper half of the front and on the vertex weaker and very widely spaced. First four antennal segments in a ratio of about 37:8:8:10, segments three slightly wider than long, segment four slightly longer than wide, segment eleven 1.3 x as long as wide. (Fig. 12.)

Pronotal disc about 1.7 x as long as mesoscutum, strongly polished and with small, widely spaced punctures; mesoscutum very weakly alutaceous, with a strong transverse depression; notauli complete, diverging and attenuate toward the front; scutellar groove slender, deflected backward at each end. Propodeal disc 1.5 x as wide as long, with five carinae between which it is strongly transverse striate, the disc elsewhere smooth and shining; declivity alutaceous, without transverse ridges; side-pieces very finely longitudinally striate. Mesopleurum polished, with scattered small punctures; upper fovea small, only slightly longer than high; lower fovea rather strongly defined except upper margin indistinct on the middle third (Fig. 30). Front femora 2.2 x as long as wide; middle tibiae strongly spinose; claws with the tooth short but sloping outward strongly (Fig. 58).

Remarks. — This species is closely related to the preceding and may only be an extreme variant of it. However, the only known specimen is from a locality far south of the southernmost record for *quinquelineatus* (Nicaragua).

MUSCARIUS SPECIES-GROUP

To this group I assign seven species, four of them without metallic colors, the other three with the head and thorax weakly to strongly reflecting blue or blue-green. The head of the female is strongly developed below the eyes as in the preceding group, the antennae arising well below the bottoms of the eyes. However, the third antennal segment of the male is very much shorter than in that group. The claws are dentate or weakly bifid, the scutellar groove variable and generally somewhat intermediate between that of the preceding and the following species-groups. The mandibles of the female have a strong preapical tooth on the lower margin.

29. RHABDEPYRIS (CHLOREPYRIS) MUSCARIUS (Westwood)

Epyris muscarius Westwood, 1874, Thesaurus Ent. Oxoniensis, p. 159, pl. 29, fig. 8 [Type: ♂, BRAZIL: Amazonia, 1861 (Bates) (HCOU)].

Rhabdepyris microstoma Kieffer, 1910, Ann. Soc. Ent. France, 78: 296-297 [Type: ♂ (not ♀ as stated), BRAZIL: Pará (C. F. Baker) (Pomona Coll.)]. New synonymy.

Rhabdepyris (*Rhabdepyris*) *microtoma* [*sic*] Kieffer, 1914, Das Tierreich, 41: 361-362.

Rhabdepyris (*Rhabdepyris*) *muscarius* Kieffer, 1914, *ibid.*, p. 362.

Plesiallotype: ♀, BRAZIL: Chapada, August (Acc. no. 2966) [CM].

Description of female plesiallotype.—Length 6.0 mm; LFW 4.0 mm. Black except extreme tip of abdomen suffused with brownish; palpi light brown, mandibles rufo-testaceous, black toward base; scape dark brownish fuscous, flagellum brown, darker above than below; tegulae testaceous; coxae black, femora dark brown, legs otherwise light castaneous; wings lightly tinged with yellowish brown, veins yellowish brown, stigma dark brown. Body setae light golden brown, short but rather conspicuous against the black integument. Mandibles with six teeth, the basal three teeth small, the next tooth broad, deeply separated from the large apical tooth, also with a sharp tooth on the outer margin at the base of the apical tooth (Fig. 50). Clypeus very short, angulate apically, the angle slightly greater than a right angle. WH 1.08 x LH; front broad, WF .66 x WH, 1.33 x HE; ocelli in about a right triangle, OOL 1.5 x WOT. Vertex broad, nearly straight, distance from eye tops to vertex crest only about one-third x HE. Front shining, barely alutaceous, punctures small, separated by 3-5 x their own diameters. Antennae arising from below frontal lobes, well below bottoms of eyes; first four antennal segments in a ratio of about 37:9:6:12, segment three .7 as long as wide, segment four 1.2 x as long as wide. (Fig. 13.)

Thoracic dorsum shining like the front, punctures small and sparse; pronotum 1.6 x as long as mesoscutum; mesoscutum transversely depressed on sides; notauli broad, attenuate and diverging toward the front; parapsidal furrows linear, extending for half the length of the mesoscutum; scutellar furrow very slender, slightly enlarged at each end. Propodeal disc 1.4 x as wide as long, with five discal carinae between which it is transversely striate, elsewhere smooth except for foveolate grooves along the lateral and posterior carinae; declivity striate only on the lower third; side-pieces shining, with only very fine sculpturing. Mesopleurum weakly alutaceous, with a few small punctures; lower fovea broadly incomplete above (Fig. 31). Front femora very strongly incrassate, only 1.8 x as long as wide; middle and hind tibiae spinose; claws dentate (Fig. 59).

Description of male type.—Length 5.5 mm; LFW 3.3 mm. Black; palpi and mandibles largely testaceous; antennae light castaneous, both scape and flagellum suffused with fuscous on the upper side; tegulae testaceous; legs pale castaneous, except the front coxae fuscous, the other coxae and all the femora suffused with brownish; wings lightly, uniformly tinged with brownish, the veins and stigma light brown. Body with rather coarse, pale setae. Clypeus forming a sharp obtuse angle, the median ridge not arched in profile. Head 1.12 x wide as high; front broad, WF .64 x WH, 1.25 x HE; OOL 1.12 x WOT; front angle of ocellar triangle slightly less than a right angle; ocelli moderately large, the hind ocelli separated from the vertex crest by about their own diameters. Vertex passing straight across only a short distance above the eyes, distance from eye tops to vertex crest less than WOT. Front strongly polished, non-alutaceous except weakly so near the bottom, with minute punctures which are separated by 3-4 x their own diameters, except more crowded below. Antennae arising slightly below bottoms of eyes, first four antennal segments in a ratio of about 18:8:5:9, segment three .8 x as long as wide, segment four 1.5 x as long as wide, segment eleven about twice as long as wide; flagellum with rather coarse, semi-erect setulae and a few fully erect setae. (Fig. 19.)

Thoracic dorsum polished, non-alutaceous, the punctures very small; maximum width of pronotal disc nearly twice its median length, the latter 1.3 x the median length of the mesoscutum; notauli strong on the posterior two-thirds of the mesoscutum, continued to the front margin only as thin lines; basal scutellar groove deep but thin, slightly expanded and deflected backward on each side. Propodeal disc 1.6 x as wide as long; disc with five strong carinae, of which the middle three are complete and the others nearly so; surface weakly transversely ridged between the discal carinae, elsewhere very smooth and polished; sublateral carina absent, but the extreme sides with a narrow groove; posterior angles foveolate. Mesopleurum shining, non-alutaceous, the upper margins of the lower fovea obsolete (Fig. 37). Middle tibiae with some fairly thick setae above, but not really spinose; claws bifid (Fig. 60).

Specimens examined. — BRAZIL: 1 ♀, 1 ♂, Chapada, March, August [CM]; 2 ♂ ♂, Pará (C. F. Baker) [Pomona Coll., CU]; 1 ♂, Amazonia (Bates) [Type, HCOU]; 2 ♀ ♀, Nova Teutonia, Santa Catarina, September, October 1957 (F. Plaumann) [Coll. G. R. Ferguson]. PERU: 1 ♂, Quincemil, Dept. Cuzco, 750 m, 16 October 1962 (L. Peña) [MCZ]. COLOMBIA: 1 ♂, Bonda, August [CM]. PANAMA: 2 ♀ ♀, Barro Colorado Isl., Canal Zone, March (Bradley, Rettenmeyer) [CU, KSU]; 1 ♂, Pacora, Canal Zone, 13 May 1953 (F. S. Blanton) [USNM]. COSTA RICA: 1 ♂, La Fortuna, San Carlos, Alajuela Prov., 19 February 1964 (H. E. Evans) [MCZ]. MEXICO: 1 ♂, Atoyac, Veracruz, April (H. H. Smith) [BMNH].

Variation. — Although I did not compare the types of *muscarius* and *microstoma* directly, my notes leave little doubt that they represent the same species; the type of *microstoma* is slightly smaller (LFW 2.8 mm). The males from Chapada and from Quincemil, Peru, are larger (LFW 3.7 mm) but very similar in all details. The males from Colombia, Panama, Costa Rica, and Mexico are unusually small (LFW 2.2-2.8 mm) and have a relatively more elongate propodeum (1.3-1.5 x as wide as long) and a slightly broader front (WF 1.3-1.4 x HE). The Panama specimen has the apical third of the abdomen rufous, while the Colombia specimen has the antennae wholly testaceous.

One of the Santa Catarina females is rather small (LFW only 3.0 mm) but is colored like the plesiallotype and has similar standard measurements. The other is larger (LFW 4.7 mm) and has the front femora wholly bright ferruginous, the head somewhat longer (WH 1.02 x LH), the front broad (WF 1.45 x HE), the propodeal disc only 1.3 x as wide as long. The Panama females also differ slightly from the plesiallotype. Both have the apical third of the abdomen rufous, the head a little less broad (WH 1.02 x LH), the front wider (WF 1.40-1.47 x HE), the propodeum less broad (1.30-1.35 x as wide as long). However, the mandibles and all other important features agree well with the plesiallotype. These females are comparable to the plesiallotype in size (LFW 3.8, 4.2 mm) even though the males from this area are very small. It is possible that I am confusing more than one species under the name *muscarius*, but I do not think so. Much of the variation parallels the variation in *luteipennis*.

30. Rhabdepyris (Chlorepyris) puncticeps new species

Holotype. — ♂, BRAZIL: Nova Teutonia, Santa Catarina, February 1963 (F. Plaumann) [MCZ, No. 30,952].

Description of male type. — Length 5.0 mm; LFW 3.8 mm. Body shining black except apical two abdominal segments suffused with reddish brown; palpi straw colored; mandibles black except apical third testaceous, teeth rufous; antennae wholly light brown below, dark brownish fuscous above except segments two and three wholly castaneous; tegulae light brown; coxae and middle and hind femora black, hind tibiae somewhat infuscated, legs otherwise bright rufo-castaneous; wings faintly tinged with yellowish brown, apical half of fore wing slightly more heavily clouded. Body setae rather coarse, light brown. Clypeus forming a sharp right angle, its median carina not arched in profile. Head 1.07 x as wide as high; WF .67 x WH, 1.36 x HE; OOL 1.10 x WOT, the front angle of the ocellar triangle very slightly less than a right angle. Vertex passing straight across a short distance above eye tops. Front strongly polished, non-alutaceous except weakly so below, wholly covered with strong punctures which are separated by 1.5-3 x their own diameters, except rather sparse in front of the anterior ocellus. First four antennal segments in a ratio of about 26:8:5:15, segment three nearly twice as wide as long, segment four about 1.5 x as long as wide, segment eleven 2.2 x as long as wide. (Fig. 20.)

Thoracic dorsum wholly polished and non-alutaceous, punctures small but quite strong, rather sparse on the mesoscutum and absent from the center of the scutellar disc; notauli strong on the posterior two-thirds of the mesoscutum, continued to the front margin as thin lines; basal scutellar groove deep but thin, slightly expanded and deflected backward at each end. Propodeal disc 1.45 x as wide as long, with five strong carinae laterad of which it is smooth and polished; declivity with numerous transverse ridges; side-pieces weakly aciculate. Mesopleurum shining, non-alutaceous, with sparse punctures, the upper margins of the lower fovea obsolete except at the ends. Front femora 2.15 x as long as wide; middle tibiae not spinose; claws bifid.

Remarks. — This species is known to me from the type only.

31. RHABDEPYRIS (CHILOREPYRIS) ORIGENUS Kieffer

Rhabdepyris origenus Kieffer, 1911, Ann. Soc. Sci. Bruxelles, 35: 222 [Type: ♀, MEXICO: Chilpancingo, Guerrero, 4600 feet, June (H. H. Smith) (BMNH)]. — Kieffer, 1914, Das Tierreich, 41: 359.

Description of female type. — Length 5.3 mm; LFW 3.3 mm. Black, except tip of abdomen suffused with dark brown; palpi light brown; mandibles ferruginous except black at base; antennae ferruginous except under side of flagellum infuscated for its entire length; legs bright ferrugino-castaneous except coxae strongly infuscated; wings subhyaline. Mandibles essentially as described and figured for *muscarius* (Fig. 50). Clypeus forming a rather sharp angle medially, with a strong median ridge. WH 1.08 x LH; WF .66 x WH, 1.20 x HE; ocelli in a right triangle close to vertex crest, OOL 1.20 x WOT. Vertex passing straight across a short distance above the eye tops, distance from eye tops to vertex crest only about one-third x HE. Front uniformly alutaceous, moderately shining, punctures small but numerous, separated by 1.5-2.5 x their own diameters. First four antennal segments in a ratio of about 36:10:6:11, segment three 0.7 x as long as wide, segment eleven 1.1 x as long as wide.

Pronotal disc about 1.5 x as long as mesoscutum, shining and weakly alutaceous, with small punctures. Mesoscutum with the notauli complete, linear, diverging anteriorly; parapsidal furrows also linear, extending for about half the length of the scutum; scutellar groove slender, slightly widened and deflected backward at each end. Propodeal disc 1.4 x as wide as long, with five carinae, the disc transversely striate between the carinae, elsewhere merely weakly alutaceous; declivity transversely striate below; side-pieces polished and with only some very fine surface sculpturing. Mesopleurum weakly alutaceous, weakly punctate; upper fovea small, lower fovea not at all defined on the upper margin (Fig. 32). Front femora greatly swollen, 1.7 x as long as their greatest width; claws dentate; middle tibiae moderately spinose.

Additional specimen examined. — MEXICO: 1 ♀, San Blas, Nayarit, 22 March 1962 (F. D. Parker) [UCD].

Variation. — The Nayarit female is of the same size as the type, but differs slightly in color: the apical 2.5 segments of the abdomen are ferruginous, the antennae somewhat lighter and more uniformly ferruginous than in the type. Standard measurements of this specimen are as follows: WH 1.03 x LH, WF 1.33 x HE, OOL 1.30 x WOT; propodeum 1.22 x as wide as long.

32. Rhabdepyris (Chlorepyris) vesculus new species

Holotype. — ♂, BRAZIL: Nova Teutonia, Santa Catarina, 14 January 1962 (F. Plaumann) [MCZ, No. 30,953].

Description of male type. — Length 4.6 mm; LFW 2.8 mm. Entirely black; palpi testaceous; mandibles testaceous except black at extreme base, teeth rufous; antennae testaceous except scape somewhat infuscated, especially above, flagellum slightly darker on the upper side than below; tegulae testaceous; coxae black, femora dark brownish fuscous, trochanters and hind tibiae somewhat infuscated, legs otherwise testaceous; wings subhyaline, veins and stigma brown. Mandibles with five teeth, the basal four teeth small and sharp; clypeus obtusely angulate, with a median ridge which is not arched in profile. Head rather broad, WH 1.10 x LH; WF .66 x WH, 1.35 x HE; ocelli moderately large, in about a right triangle, the posterior ocelli slightly less than their own diameters from the vertex crest; OOL 0.90 x WOT. Vertex very broadly rounded, almost straight; distance from eye tops to vertex crest about one-third x HE. Front wholly alutaceous, moderately shining, with small punctures which are separated by 1.5-2.5 x their own diameters, except sparse in front of ocellar triangle. Antennae arising well below bottoms of eyes, unusually short, first four segments in a ratio of about 15:5:4:6, segment three .6 x as long as wide, segment four about as long as wide, segment eleven 1.4 x as long as wide; flagellar pubescence semi-erect, pale. (Fig. 22.)

Thoracic dorsum alutaceous and with small punctures like the front; pronotum about 1.6 x as long as the mesoscutum; notauli rather wide, much tapered and divergent anteriorly; scutellar groove relatively short and wide, much wider on the sides than medially. Propodeal disc 1.3 x as wide as long, with five discal carinae and also with two more rounded ridges on each side between the lateral discals and the laterals, the surface rather irregularly transversely striate between the carinae and ridges, wholly covered with sculpturing; declivity and side-pieces both with strong horizontal ridges. Mesopleurum weakly alutaceous, without distinct punctures; lower fovea very broadly open above; upper fovea elongate, opening downward posteriorly (Fig. 38). Front femora 2.3 x as long as wide; middle femora not spinose; claws dentate, the tooth acute, sloping outward somewhat (Fig. 61).

Paratypes. — BRAZIL: 5 ♂♂, same data as type except September, November, December, January, 1951, 1962, 1963 [MCZ, USNM, Coll. G. R. Ferguson].

Variation. — The paratypes are very similar to the type in color except that the antennae tend to be darker in some specimens, wholly dull brownish in one. The sculpturing is very similar except that one specimen has only one ridge between the lateral discal and lateral carinae of the propodeum, leaving a narrow smooth area on each side. LFW varies from 2.3 to 2.8 mm; WH/LH varies from 1.07 to 1.10; WF/HE varies from 1.28 to 1.44 x HE; the propodeal disc varies from 1.28 to 1.33 x as wide as long. Throughout the series WOT exceeds OOL very slightly.

33. Rhabdepyris (Chlorepyris) virescens new species

Holotype. — ♀, BRAZIL: Nova Teutonia, Santa Catarina, August 1963 (F. Plaumann) [MCZ, No. 30,954].

Description of female type. — Length 6.0 mm; LFW 4.3 mm. Head and thorax black, with dull olive-green reflections; propodeum black: abdomen shining black except the apical two segments suffused with rufo-testaceous; palpi straw-colored; mandibles rufo-castaneous except black at extreme base; scape bright rufo-castaneous, flagellum light brown below, somewhat dusky above; tegulae testaceous; legs bright ferruginous except front and hind coxae black, middle coxae and front and hind femora partially suffused with black; wings lightly infuscated, the fore wing with a darker cloud below the marginal cell; veins brown except testaceous toward base of wing. Mandibles with a small subapical tooth on the lower margin, a large apical tooth, and four small teeth which are close together and separated from the apical tooth by a small cutting edge (Fig. 51). Clypeus obtusely angulate, its median ridge nearly straight in profile. WH 1.02 x LH; front broad, WF .69 x WH, 1.30 x HE; front angle of ocellar triangle very slightly less than a right angle, OOL 1.40 x WOT. Vertex passing straight across, distance from eye tops to vertex crest only .3 x HE. Front shining, weakly alutaceous, with very small punctures which are separated by 3-5 x their own diameters. Antennae arising from below frontal lobes, well below bottoms of eyes; first four segments in a ratio of about 20:5:4:6, segment three .8 as long as wide, segment four 1.2 x as long as wide, segment eleven 1.3 x as long as wide. (Fig. 14.)

Pronotum weakly alutaceous and with small punctures like the front, the median length of the disc nearly twice that of mesoscutum. Mesoscutum slightly more strongly alutaceous than pronotum, with small punctures, weakly transversely depressed; notauli rather wide, diverging and attenuate anteriorly, reaching anterior margin only as thin lines; scutellar groove rather slender, deflected sharply backward and expanded at each end. Propodeal disc 1.3 x as wide as long, with five discal carinae between which it is strongly transversely striate, between the lateral discals and lateral carinae smooth and very weakly alutaceous; declivity with strong transverse ridges on lower half; side-pieces smooth except very finely alutaceous. Mesopleurum weakly alutaceous, very weakly punctate; upper fovea ovoid, slightly longer than high; lower fovea broadly incomplete above (Fig. 33). Front femora twice as long as wide; middle tibiae spinose; claws dentate (Fig. 62).

Allotype. — ♂, BRAZIL: same data as type except December, 1962 [MCZ].

Description of male allotype. — Length 4.5 mm; LFW 3.0 mm. Head and thorax shining black, with a weak bluish green cast; propodeum black; abdomen shining black, the apical two segments suffused with brownish; palpi straw-colored; mandibles testaceous except black at base, the teeth rufous; antennae pale castaneous except scape fuscous above, flagellum slightly infuscated above; tegulae testaceous; coxae black, femora dark brown, legs otherwise testaceous; wings very lightly tinged with brownish, somewhat more evidently so around the radial vein. Mandibles and clypeus not differing noticeably from those of *vesculus;* head much wider than high, WH 1.08 x LH; WF .68 x WH, 1.40 x HE; ocelli moderately large, in about a right triangle, OOL and WOT subequal. Vertex broadly rounded; distance from eye tops to vertex crest equal to about one-third x HE. Front strongly polished, barely alutaceous, the punctures minute and inconspicuous. First four antennal segments in a ratio of about 18:6:5:8, segment three .7 as long as wide, segment four approximately as long as wide, segment eleven about twice as long as wide; flagellar pubescence semierect, about .2 as long as width of flagellar segments. (Fig. 21.)

Pronotal disc slightly longer along midline than mesoscutum, obscurely alutaceous and with very small punctures. Mesoscutum strongly polished, wholly covered with minute setigerous punctures; notauli rather wide, diverging and strongly attenuated anteriorly; scutellar groove fairly wide, broadened and deflected backward at each end; center of scutellar disc polished and impunctate. Propodeal disc 1.4 x as wide as long, with five discal carinae between which it is irregularly transversely ridged; space laterad of lateral discals filled with transverse striae which are obsolescent behind; lateral and sublateral carinae present, each subtending a somewhat foveolate groove; declivity transversely ridged; side-pieces with irregular longitudinal striae which tend to be coarser below. Mesopleurum shining, obscurely alutaceous and punctate; upper fovea large and continuing on down the posterior margin of the mesopleurum; lower fovea fairly well defined, but its upper margin obsolete on the middle third (Fig. 39). Front femora 2.2 x as long as wide; claws dentate, the tooth sloping outward (Fig. 63).

Paratypes. — BRAZIL: 5 ♀♀, 12 ♂♂, same data as type except various dates, February, March, April, June, September-December, 1938, 1952, 1953, 1961, 1962, 1964 [MCZ, BMNH, BSA, Coll. G. R. Ferguson]; 1 ♂, Corumba, May [ANSP]; 1 ♂, Santarem (no further data) [USNM]. PERU: 1 ♂, Upper Rio Pachitea, 21 July 1920 (Cornell U. Exp.) [CU]. ECUADOR: 1 ♂, Ongota, 8 km SE Tena, May 1963 (L. Peña) [MCZ]. PANAMA: 1 ♀, Puerto Bello, 21 February 1911 (E. A. Schwarz) [USNM]; 1 ♂, Barro Colorado Isl., Canal Zone, 18 July 1956 (C. W. & M. E. Rettenmeyer) [KSU].

Variation. — The topotypic female paratypes vary considerably in size (LFW 3.3-4.0 mm); WH varies from 1.00 to 1.02 x LH. The amount of infuscation of the femora is somewhat variable, but otherwise there is close agreement with the type. The Panama female has the apical .4 of the abdomen bright ferruginous; in this specimen LFW is 3.8 mm, WH/LH is 1.02, WF/HE 1.17. Otherwise the resemblance to the type is close.

The males show considerable variation and I concede the possibility that more than one species may be involved. LFW varies from 2.8 to 3.7 mm. Color of the head and thorax varies from olive-green through blue-green to a shining, metallic blue; the intensity of the metallic reflections also varies considerably. In some of the topotypes, WOT exceeds OOL slightly; in one of them the front legs are wholly pale ferruginous, while in others the legs are mostly blackish and the antennae darker than in the allotype. The Panama male has the apical third of the abdomen bright ferruginous. This specimen and those from Peru, Ecuador, and Santarem have the front relatively narrow (WF 1.15-1.25 x HE), but in the Corumba specimen the front is broad (WF 1.40 x HE); in fact the head itself is unusually broad (WH 1.20 x LH). The last-named specimen also has relatively coarser sculpturing on the propodeum, especially on the side-pieces, and in lateral view the anterior margins of the foveae on the posterior angles can be seen to be produced upward as tooth-like processes. However, tendencies in these directions can be seen in the Panama specimen; indeed, there is much variation in details of propodeal sculpturing throughout the entire series, although the shape of the propodeal disc is quite constant (1.35-1.45 x as wide as long).

The variation in the color of the abdomen in this species parallels similar variation in *luteipennis* and *muscarius*, and the other variation is not inconsistent with the patterns in those species.

34. RHABDEPYRIS (CHLOREPYRIS) VIRIDIS (Cameron)

Epyris viridis Cameron, 1888, Biol. Centr.-Amer., Hymen. I, p. 451 [Type: ♀, GUATEMALA: San Juan, Vera Paz (G. C. Champion) (BMNH)].
Rhabdepyris viridis Kieffer, 1908, Gen. Insect., 76:32.
Anisepyris viridis Kieffer, 1914, Das Tierreich, 41: 439.

Description of female type. — Length 5.5 mm; LFW 3.0 mm. Head, pronotum, and mesopleura bright bluish green; mesonotum bright blue; propodeum black; abdomen shining black except each segment with a narrow, apical testaceous band (more noticeable ventrally) and the apical 1.5 segments mostly testaceous; palpi light brown; mandibles blackish; antennae black, scape with green reflections; middle and hind coxae and femora dark brownish-fuscous, with weak metallic reflections; tibiae and tarsi medium brown; wings subhyaline, with a faint yellowish tinge, with a strong brownish cloud just below the stigma and radial vein. Mandibles appearing tridentate, but probably not differing materially from those of related species. Clypeus with an angulate median lobe. Head about as wide as high; inner orbits subparallel below, WF .69 x WH, 1.18 x HE; ocelli in a compact triangle, front angle much less than a right angle; OOL 1.4 x WOT. Vertex passing straight across a distance above eye tops equal to about .3 x HE. Front uniformly but very weakly alutaceous, strongly shining, punctures strong, separated by 2-3 x their own diameters. First four antennal segments in a ratio of about 32:10:7:10, segment three slightly wider than long, segment eleven about as long as wide.

Pronotal disc .57 x as long as its posterior width, 1.25 x as long as mesoscutum; surface of pronotum shining, like the front, but the punctures somewhat weaker than on the front. Mesoscutum also shining, with a few punctures on the posterior half but otherwise smooth, not depressed; notauli complete, diverging and becoming more slender anteriorly; scutellar groove widened and deflected backward on each end. Propodeal disc only 1.15 x as wide as long, with five strong carinae, the surface transversely striate between the carinae, elsewhere shining; declivity transversely striate, more especially below. Mesopleurum alutaceous although somewhat shining; upper fovea small, lower fovea large, broadly incomplete above (essentially as in *virescens*, Fig. 33). Claws dentate; front femora 1.8 x as long as their greatest width.

Remarks. — This distinctive species has not been recovered since its description in 1888.

35. RHABDEPYRIS (CHLOREPYRIS) METALLICUS Kieffer

Rhabdepyris metallicus Kieffer, 1908, Ann. Soc. Sci. Bruxelles, 32: 10 [Type: ♀, NICARAGUA: Granada (? location of type)]. —Kieffer, 1914, Das Tierreich, 41: 360.

Original description (translated and paraphrased). — Length 4 mm. Head metallic blue, pro- and mesonota metallic green with bluish reflections; abdomen black except last two segments red; mandibles and palpi red; scape blackish brown, antennae otherwise red; legs red except coxae black; wings brownish. Head subcircular, smooth and shining, with dense, fine punctures. Eyes separated from vertex crest by about one-third x HE. Third and fourth antennal segments somewhat transverse, the following segments thicker, at first transverse, then somewhat longer. Thoracic dorsum shining; pronotum punctate like the head; mesoscutum somewhat shorter than pronotum, almost impunctate; notauli wide on the posterior part, divergent and becoming very thin anteriorly. Scutellum impunctate, its groove broad and arcuate. Propodeum hardly transverse, with five discal carinae of which the middle three are parallel, the lateral ones oblique.

Remarks. — I have not been able to locate the type of this species, and I have not been able to recognize the species from the description. I would judge it to be closely related to the preceding and the following species. The metallic colors are apparently much more intense than in *subviridis*, the antennae and legs much lighter in color than in *viridis*.

VIRIDISSIMUS SPECIES-GROUP

This group includes six brilliantly green or blue species, all having the scutellar groove in the form of paired pits connected by a slender groove (*Chlorepyris* in the sense of Kieffer). The head is much wider than high in both sexes and is little developed anteriorly, the antennae arising only slightly below the bottoms of the eyes. It is possible that *metallicus* Kieffer belongs here, but since Kieffer states that the head of that species is "fast kreisrund," I assume that it may belong near *viridis* in the preceding species-group. In the *viridissimus* group the claws of the male tend to be more or less trifid; however, there is no sharp morphological gap between the males of these two species-groups.

36. Rhabdepyris (Chlorepyris) subviridis (Kieffer) new combination

Epyris subviridis Kieffer, 1911, Ann. Soc. Sci. Bruxelles, 35: 225-226 [Type: ♂, MEXICO: Teapa, Tabasco, March (H. H. Smith) (BMNH)].

Chlorepyris subviridis Kieffer, 1913, Boll. Lab. Zool. Portici, 7: 108. — Kieffer, 1914, Das Tierreich, 41: 415.

Plesiallotype. — ♀, PANAMA: Pacora, Canal Zone, 14 May 1953 (F. S. Blanton) [USNM].

Description of female plesiallotype. — Length 5.5 mm; LFW 3.5 mm. Head and thorax black, with dull olive-green reflections; propodeum black; abdomen shining black, apical .4 ferruginous; palpi straw-colored; mandibles light castaneous, the teeth darker; antennae uniformly light castaneous; tegulae testaceous; coxae black; hind femora and outer side of front femora dark brown, legs otherwise testaceous; wings faintly tinged with yellowish brown, slightly darker around the radial vein, veins yellowish toward base of wing. Mandibles with a large subapical tooth on the lower margin, otherwise with five teeth, the basal three teeth small and rounded (Fig. 52). Clypeus obtusely subangulate, extending barely beyond the antennal insertions. WH 1.10 x LH; WF .62 x WH, 1.06 x HE; front angle of ocellar triangle much less than a right angle, OOL 1.6 x WOT. Vertex nearly straight, distance from eye tops to vertex crest about one-third x HE. Front strongly shining, very weakly alutaceous, the punctures strong, separated from one another by 1-3 x their own diameters below, much more widely spaced above. Antennae arising only slightly below bottoms of eyes, first four segments in a ratio of about 28 :7 :5 :10, segment three about .6 as long as wide, segment four slightly longer than wide, segment eleven about as long as wide. (Fig. 15.)

Thoracic dorsum alutaceous, not as strongly shining as the front, the punctures small and well spaced; pronotum about 1.25

x as long as mesoscutum along midline. Notauli elongate, attenuate and diverging anteriorly; scutellar groove very narrow medially, connecting two oblique, elliptical pits. Propodeal disc 1.30 x as wide as long, with five discal carinae, smooth and polished between the lateral discals and the laterals; declivity polished, with some transverse ridges below; side-pieces shining and with very fine surface sculpturing. Mesopleurum alutaceous and with numerous small punctures; upper fovea small, slender; lower fovea broadly incomplete above (Fig. 34). Front femora 2.1 x as long as wide; middle tibiae spinose; claws dentate, the tooth fairly long and sloping outward somewhat.

Description of male type. — Length 5.0 mm; LFW 2.8 mm. Head and thorax black, with moderately intense dark blue-green reflections; propodeum black; abdomen shining black except apical two segments suffused with brown; palpi and mandibles straw-colored, the mandibular teeth rufous; antennae light castaneous, all except the apical segment somewhat infuscated above, scape especially so; tegulae testaceous; legs bright rufo-castaneous except all coxae blackish; wings subhyaline, veins and stigma brown. Mandibles with the usual five teeth; clypeus obtusely subangulate, with a low median ridge. WH 1.18 x LH; WF .70 x WH, 1.43 x HE; front angle of ocellar triangle slightly less than a right angle, OOL 1.10 x WOT. Vertex broadly rounded off a short distance above the eye tops. Front strongly shining, weakly alutaceous, punctures small but sharply defined, on lower part separated by 2-3 x their own diameters, on upper part by 4-6 x their own diameters. First four antennal segments in a ratio of about 20:10:6:11, segment three .6 as long as wide, segment four about as long as thick, segment eleven 2.5 x as long as thick; flagellar pubescence pale and erect, longest setulae of segment eleven about half as long as width of segment (Fig. 73).

Thoracic dorsum shining, weakly alutaceous, the punctures weak; pronotal disc slightly longer than mesoscutum; notauli very wide behind, much narrowed anteriorly, reaching anterior margin of scutum as thin lines; scutellar groove wider medially than in the female, widened and deflected backward at each end. Propodeal disc 1.35 x as wide as long, with five discal carinae, only the median one intercepting the transverse carina; lateral and sublateral carinae strong, disc also with a round-topped ridge between the sublaterals and the lateral discals and mostly covered with transverse striae; declivity transversely ridged below; side-pieces with strong longitudinal ridges, more especially below. Mesopleurum shining, weakly alutaceous; upper fovea open behind, as in the preceding species; lower fovea broadly open above. Claws trifid (Fig. 65).

Other specimens examined.—HONDURAS: 1 ♀, "Banana debris, 3-25-40, lot no. 40-6469" (presumably intercepted at quarantine) [USNM]. COSTA RICA: 1 ♂, Turrialba, 17 June 1949 (K. W. Cooper) [USNM]. PANAMA: 2 ♂♂, Pacora, Canal Zone, same data as plesiallotype except 13 May 1953 and July 1953 [USNM].

Variation.—The Honduras female is strikingly like the female from Panama; WF is 1.13 x HE; OOL is 1.53 x WOT; the upper mesopleural fovea is even more elongate. The males are all slightly larger than the type (LFW 3.2-3.3 mm); the Pacora specimens have paler antennae, only very slightly infuscated above, and these specimens also have the hind femora infuscated. In the males, WH varies from 1.13 to 1.18 x WH, WF from 1.33 to 1.38 x HE, OOL from 1.13 to 1.22 x WOT. In the Pacora males the antennae are more elongate than in the Turrialba and Teapa males, segment four being distinctly longer than wide, segment eleven more than 3 x as long as wide.

37. RHABDEPYRIS (CHILOREPYRIS) BLANTONI new species

Holotype.—♂, PANAMA: Pacora, Canal Zone, 13 May 1953 (F. S. Blanton) [USNM, No. 67,541].

Description of male type.—Length 5.5 mm; LFW 3.8 mm. Head and thorax black, shining, with moderately strong bluish green reflections; propodeum black, with faint dark blue reflections in certain lights; abdomen shining black, the apical .4 bright ferruginous; palpi and mandibles testaceous, the latter dark at tips; antennae bright rufo-testaceous except the scape strongly infuscated; tegulae testaceous; coxae black, femora medium brown, legs otherwise testaceous; wings lightly tinged with brownish, veins and stigma brown. Mandibles with the usual five teeth; clypeus short, obtusely angulate. WH 1.09 x LH; WF .62 x WH, 1.10 x HE; ocelli in about a right triangle, OOL 1.1 x WOT. Front shining, weakly alutaceous except not at all so on the vertex, with sharply defined punctures which are separated by only 1-2 x their own diameters. First four antennal segments in a ratio of about 28:7:4:11, segment three unusually short, only about .3 as long as wide, segment four very slightly longer than wide, segment eleven about 1.5 x as long as wide. (Fig. 23.)

Thoracic dorsum polished, non-alutaceous, wholly covered with small punctures; notauli moderately wide behind, tapering and diverging anteriorly; scutellum with a pair of large, strongly oblique pits which are connected by a slender groove. Propodeal disc 1.4 x as wide as long, with five carinae; lateral and sublateral carinae running closely parallel, the latter paralleled by a broad, longitudinal groove; space between this groove and the lateral discal carinae shining and with only some very weak surface sculpturing; declivity with transverse ridges below; side-pieces with moderately coarse longitudinal striae. Mesopleurum polished, punctate; upper fovea elongate, open behind; lower fovea large, its upper margin obsolete (Fig. 40). Front femora 2.3 x as long as wide; middle tibiae weakly spinose; claws trifid, the middle ray truncate (Fig. 64).

Paratypes. — PANAMA: 5 ♂♂, same data as type [USNM, MCZ].

Variation. — Little variation is evident in this series. There is some slight variation in the hue of the metallic colors of the head and thorax and in the degree of infuscation of the femora; in some specimens the bluish reflections of the propodeum are barely evident. In the paratypes, LFW varies from 3.1 to 3.5, WH from 1.06 to 1.09 x LH, WF from 1.1 to 1.2 x HE, OOL from 1.0 to 1.1 x WOT.

Remarks. — It is possible that these specimens represent the male sex of *metallicus* Kieffer or *tricolor* n.sp., but there are enough doubts in my mind to justify recognizing them as a distinct species for the present. The very short third antennal segment is unique in this subgenus.

38. RHABDEPYRIS (CHLOREPYRIS) VIRIDISSIMUS (Kieffer) new combination

Epyris viridis Kieffer, 1911, Ann. Soc. Sci. Bruxelles, 35: 223-225 [Type: ♀, MEXICO: Teapa, Tabasco, March (H. H. Smith) (BMNH)]. Preoccupied by Cameron, 1888.

Epyris viridissimus Kieffer, 1911, *ibid.*, p. 225 [Type: ♂, MEXICO: Teapa, Tabasco, March (H. H. Smith) (BMNH)].

Chlorepyris semiviridis Kieffer, 1913, Boll. Lab. Zool. Portici, 7: 108 (new name for *viridis* Kieffer, not Cameron). —Kieffer, 1914, Das Tierreich, 41: 414. New synonymy.

Chlorepyris viridissimus Kieffer, 1914, *ibid.*, p. 415.

Description of female type of semiviridis Kieffer. — Length 7.8 mm; LFW 4.4 mm. Head and thorax brilliant green; propodeum black; basal 3.5 segments of abdomen shining black, remainder of abdomen bright rufo-castaneous; palpi light brown; mandibles ferruginous; antennae bright rufo-castaneous, slightly paler apically than basally; tegulae with greenish reflections; legs bright rufo-castaneous except all coxae suffused with black; fore wing lightly tinged with yellowish, basal third and apical .4 lightly infuscated, leaving a subhyaline area below the stigma. Mandibles with five apical teeth and a strong subapical tooth on the lower margin (Fig. 53). Clypeus short, obtusely angulate, its median ridge slightly concave in profile. WH 1.2 x LH; WF .61 x WH, 1.10 x HE; ocelli in a small triangle, front angle less than a right angle, OOL 1.4 x WOT. Front polished, obscurely alutaceous, punctures strongly defined, separated by 2-4 x their own diameters. First four antennal segments in a ratio of about 22:6:5:7, segment three about .7 x as long as wide, segments four and eleven each about as long as wide.

Thoracic dorsum shining, obscurely alutaceous, and with well spaced strong punctures like the front; notauli moderately wide behind, tapering and diverging anteriorly; scutellar groove relatively narrow, deflected backward and slightly widened at each end. Propodeal disc 1.4 x as wide as long, the five discal carinae all reaching the transverse carina; lateral and posterior carinae margined within by broad, subfoveolate grooves; surface transversely ribbed between discal carinae, elsewhere with weak sculpturing. Mesopleurum polished, weakly alutaceous, with small, well-spaced punctures; upper fovea about 3 x as long as high; lower fovea large, broadly open above. Front femora 2.2 x as long as wide; middle tibiae strongly spinose; claws trifid (Fig. 66).

Description of male type. — Length 6 mm; LFW 3.6 mm. Head and thorax brilliant green; propodeum black; basal 4.5 segments of abdomen shining black, remainder bright rufo-castaneous; palpi straw-colored; mandibles rufo-testaceous, the teeth darker; clypeus brownish; antennae with the scape fuscous, the flagellum pale rufo-castaneous except basal few segments weakly infuscated on upper side; tegulae brown, with blue-green reflections; legs bright rufo-castaneous except all coxae blackish; wings very lightly infuscated, more especially so around radial vein of fore wing. Mandibles 5-toothed; clypeus very short, obtusely angulate. WH 1.20 x LH; WF .61 x WH, 1.13 x HE; front angle of ocellar triangle very slightly less than a right angle, OOL 1.05 x WOT. Front shining, obscurely alutaceous, the punctures strong, somewhat more closely spaced than in the female, separated by 1-3 x their own diameters. First four antennal segments in a ratio of about 28:6:8:13, segment three about .7 as long as thick, segment four about as long as thick, segment eleven about twice as long as thick.

Thoracic dorsum weakly alutaceous, wholly covered with rather large punctures; notauli wide behind, separated by about their own widths, diverging and attenuate anteriorly; scutellar groove narrow, connecting two large, oblique pits. Propodeal disc 1.4 x as wide as long, with five discal carinae; lateral and sublateral carinae closely parallel, the latter paralleled by a shallow groove along its mesal margin; postero-lateral foveae very strong; side-pieces with 8-10 coarse, irregular ridges. Mesopleurum alutaceous, with shallow punctures; upper fovea elongate, open behind (Fig. 41); lower fovea not well defined above. Front femora 2.4 x as long as wide; claws trifid (Fig. 67).

Other specimens examined. — MEXICO: 1 ♀, Mazatlan, Sinaloa, 20 July 1959 (H. E. Evans) [MCZ]; 1 ♀, Cordoba, Veracruz, 20 January 1908 (F. Knab) [USNM]; 3 ♂♂, Teapa, Tabasco (same data as type) [BMNH]. GUATEMALA: 1 ♀, "Guatemalan forest," 3 March 1909 (F. Knab) [USNM].

Variation. — The females vary considerably in size (LFW 4.0-5.3 mm) but differ in color only in having the green coloration somewhat blue-green in the Cordoba specimen. This same specimen also has the punctures of the head and thorax somewhat weaker and more widely spaced, also the scutellar groove very narrow indeed, connecting two large, oblique pits, more as in the male. Since the other two females show some variation in the scutellar groove, I doubt if the Cordoba specimen is more than an extreme variant in this regard. The Mazatlan specimen is the largest, being fully 9 mm long, and has the thoracic dorsum and pleura much more evidently alutaceous than do the other females. In the females, WH varies from 1.3 to 1.20 x LH, WF from 1.10 to 1.25 x HE, OOL from 1.4 to 1.6 x WOT.

The three topotypic males resemble the type closely, but some are more blue-green than green, and the head tends to be slightly less broad in some (WH 1.15-1.20 x LH; WF 1.10-1.20 x HE).

39. RHABDEPYRIS (CHLOREPYRIS) FULGENS (Brues) new combination

Epyris fulgens Brues, 1907, Bull. Wisc. Nat. Hist. Soc., 5: 99-100 [Type: ♀, TEXAS: Brownsville, 4 August (C. Schaeffer) (USNM, No. 42,702)].

Chlorepyris fulgens Kieffer, 1914, Das Tierreich, 41: 414. —Muesebeck and Walkley, 1951, U.S. Dept. Agr. Monogr. 2, p. 730.

Description of female type. — Length 7.0 mm; LFW 4.0 mm. Head and thoracic dorsum green, with bluish green reflections in certain lights; mesopleurum aeneous, grading into bluish below; propodeum violaceous; basal three abdominal segments and basal part of fourth tergite black, remainder of abdomen rufo-testaceous; palpi testaceous; mandibles testaceous, the teeth rufous; antennae pale ferruginous except somewhat dusky on outer surface, segments two and three wholly dusky; tegulae with greenish reflections; legs bright rufo-testaceous except front coxae black, hind coxae weakly infuscated basally; wings subhyaline, veins and stigma light brown. Mandibles as in the preceding species and as shown in Figure 54; clypeus broadly angulate, the median ridge concave in profile. WH 1.16 x LH; WF .63 x WH, 1.23 x HE; front angle of ocellar triangle slightly less than a right angle, OOL 1.5 x WOT. Front strongly polished, obscurely alutaceous below, with a linear median impression opposite the lower third of the eyes; punctures of front strong, separated by 2-4 x their own diameters. First four antennal segments in a ratio of about 18:5:4:6, segment three considerably wider than long, segment four slightly longer than wide (Fig. 74).

Thoracic dorsum shining, obscurely alutaceous; punctures of pronotum strong, separated by 2-4 x their own diameters, those on the mesoscutum occurring mostly along the notauli; notauli linear, only slightly widened behind, complete; scutellar groove narrow, much widened on each side. Propodeal disc 1.4 x as wide as long, with five discal carinae between which it is transversely ribbed, the space between the lateral discals and the laterals smooth and merely very finely striolate; side-pieces finely striolate. Mesopleurum weakly alutaceous, with small punctures; upper fovea about twice as long as high; lower fovea broadly incomplete above. Front femora twice as long as wide: middle tibiae strongly spinose, hind tibia more weakly so; claws trifid (Fig. 68).

Plesiallotype. — ♂, HONDURAS: Tegucigalpa (F. J. Dyer) [USNM].

Description of male plesiallotype. — Length 5.5 mm; LFW 3.9 mm. Head and thorax brilliant green, with the thorax with some bluish tints; propodeum bluish green, somewhat less brilliant than the head and thorax, especially on the side-pieces; abdomen black, apical .4 rufo-testaceous; palpi and mandibles testaceous, the latter with rufous tips; scape fuscous, flagellum rufo-testaceous except basal segments moderately infuscated on upper surface; tegulae brown, with green reflections; legs bright rufo-testaceous except all coxae infuscated; wings tinged with brownish, veins and stigma brown. Clypeus obtusely angulate, its median carina concave in profile. WH 1.20 x LH; WF .63 x WH, 1.24 x HE; front angle of ocellar triangle very slightly exceeding a right angle, OOL and WOT subequal. Vertex straight across in center, broadly rounded on the sides. Front polished, obscurely alutaceous below but non-alutaceous above, punctures strong, separated by 1-3 x their own diameters. First four antennal segments in a ratio of about 25:7:8:13, segment three .7 as long as wide, segment four very slightly longer than wide, segment eleven 1.8 x as long as wide. (Fig. 24.)

Thoracic dorsum shining, wholly covered with fairly strong punctures; notauli wide behind, separated by slightly less than their own widths, strongly diverging and attenuate anteriorly; scutellar groove strong, much widened at each end. Propodeal disc 1.4 x as wide as long, with five carinae between which it is strongly transversely ridged; lateral and sublateral carinae closely parallel, the sublaterals subtending a broad groove which occupies nearly half the space between these carinae and the lateral discals; postero-lateral foveae very large; side-pieces with only about six large, longitudinal ridges. Mesopleurum with the upper fovea large, open behind; lower fovea large, well defined, its upper margin partially incomplete (Fig. 42). Front femora 2.4 x as long as wide; claws trifid, about as in *viridissimus* (Fig. 67).

Remarks. — This species is known to me only from the two specimens described above.

40. RHABDEPYRIS (CHLOREPYRIS) TRICOLOR new species

Holotype. — ♀, ECUADOR (label reads: on roses *ex* Ecuador, VII-29-1962; F. J. Formichella, lot 62-26784) (presumably intercepted at quarantine) [USNM, No. 67,542].

Description of female type. — Length 6.0 mm; LFW 3.5 mm. Head, thorax, and propodeum brilliant dark blue-green, outer side of front femora also of this color; abdomen black except apical .4 bright ferruginous; palpi and mandibles testaceous except the latter darker at extreme base and apex; antennae fuscous except segments 4-12 testaceous beneath, the apical segment wholly testaceous; coxae black, legs otherwise bright ferruginous except outer side of front femora dark like the body; wings tinged with brown, the base of the fore wing, including the veins, somewhat yellowish. Mandibles essentially as figured for the preceding species (Fig. 54). Clypeus obtusely angulate, barely protruding beyond the strong antennal lobes. WH 1.12 x LH; WF .64 x WH, 1.18 x HE; front angle of ocellar triangle less than a right angle, OOL 1.7 x WOT. Vertex straight, distance from eye tops to vertex crest equal to about one-third x HE. Front polished, very obscurely alutaceous, with strong punctures which are separated, in the center of the front, by 2-4 x their own diameters (more crowded below, less so above). Antennae arising only slightly below bottoms of eyes, first four segments in a ratio of about 30:7:6:9, segment three considerably wider than long, segment four about as long as wide, segments 5-12 very slightly wider than long. (Fig. 16.)

Thoracic dorsum shining but slightly more evidently alutaceous than the front; pronotum with numerous fairly strong punctures, slightly longer than mesoscutum. Mesoscutum with a few punctures along the parapsidal furrows and notauli, the latter complete but reduced to thin lines on the anterior half; scutellar groove a mere line connecting two oblique, elliptical pits. Propodeal disc 1.35 x as wide as long, with five discal carinae between which it is transversely striate and laterad of which there is weak surface sculpturing; sublateral carinae not distinct, but lateral carinae paralleled by a broad, transversely striate groove; declivity with transverse ridges below; side-pieces shining, with weak longitudinal aciculations. Mesopleurum weakly alutaceous, weakly punctate; upper fovea extending most of the length of the mesopleurum, nearly 5 x as long as wide; lower fovea large, its upper margin mostly indistinct (Fig. 35). Front femora moderately incrassate, measuring 2.0 x as long as wide; middle and hind tibiae strongly spinose; claws trifid (as figured for *fulgens*, Fig. 68).

Remarks. — This species is known only from the type. It seems definitely to belong to this complex of *Rhabdepyris*, although the scutellar pits differ hardly at all from those of some species of *Epyris*.

41. RHABDEPYRIS (CHLOREPYRIS) VIOLACEUS new species

Holotype. — ♀, BRAZIL: Nova Teutonia, Santa Catarina, 30 August 1938 (F. Plaumann) [BMNH].

Description of female type. — Length 7.5 mm; LFW 4.5 mm. Head and thorax, including scape, tegulae, and outer sides of femora, brilliant blue-violet, with greenish tints in certain lights; propodeum dark blue, contrasting slightly to head and thorax; abdomen black except apical tergite brownish; mandibles black except apical fourth rufo-testaceous; antennae fuscous except front tibiae and all the tarsi light brown; wings lightly tinged with brown, veins and stigma brown. Mandibles with five apical teeth and a large subapical tooth on the lower margin. Clypeus obtusely subangulate, barely produced beyond antennal insertions. WH 1.17 x LH; WF .65 x WH, 1.20 x HE; front angle of ocellar triangle much less than a right angle, OOL 1.60 x WOT. Vertex broad, straight; distance from eye tops to vertex crest equal to about .3 x HE. Front shining, weakly alutaceous, with large punctures which are separated by only 1-2 x their own diameters (more widely spaced at level of ocelli). First four antennal segments in a ratio of about 40:9:8:12, segment three very slightly wider than long, segments four and eleven both approximately as wide as long.

Thoracic dorsum weakly alutaceous and punctate like the front; notauli complete, rather slender and only slightly attenuate anteriorly; scutellar grooves very thin, connecting a pair of small lateral pits. Propodeal disc 1.35 x as wide as long, the five discal carinae parallel and complete, the surface weakly transversely ridged between the carinae, elsewhere with only very weak surface sculpturing; side-pieces shining, with extremely fine longitudinal striations. Upper mesopleural fovea about 3 x as long as high, lower fovea broadly incomplete above (Fig. 36). Front femora only slightly incrassate, measuring 2.4 x as long as wide; claws trifid, middle ray truncate (Fig. 69).

Allotype. — ♂, BRAZIL: Rio Caraguata, Matto Grosso, May 1953 (F. Plaumann) [MCZ].

Description of male allotype. — Length 6.0 mm; LFW 3.5 mm. Coloration as described for female, except with slightly stronger greenish reflections, even on the propodeum, which contrasts very little with the thorax; abdomen entirely black; mandibles brownish, paler apically; antennae fuscous except flagellar segments testaceous beneath; legs and wings colored as in female. Clypeus broadly subangulate. WH 1.18 x LH; WF .64 x WH, 1.28 x HE; ocellar triangle rather broad, WOT exceeding OOL slightly. Front polished, non-alutaceous, punctures strong, separated by 1.5-3 x their own diameters. First four antennal segments in a ratio of about 20:6:8:11, segment three considerably wider than long, segment four slightly longer than wide, segment eleven about twice as long as wide.

Thoracic dorsum slightly alutaceous, with strong punctures like the front; notauli very wide behind, separated by only a thin carina, diverging and attenuate anteriorly; parapsidal furrows strong and complete, somewhat sinuate; scutellar disc rather flat, the basal groove rather short, expanded on each side to form oblique pits. Propodeal disc 1.3 x as wide as long, somewhat narrowed behind; disc with only three carinae, between which it is transversely ridged, sublateral carinae strong, subtending a broad groove which occupies about half the space between the sublaterals and the lateral discals; this groove, like that between the sublateral and lateral carinae, is polished and without sculpturing; side-pieces with only six strong, longitudinal ridges. Mesopleurum with the upper fovea very large, open behind. Claws trifid (Fig. 70).

Paratypes. — 2 ♀♀, BRAZIL: same data as type except dated 10 September 1938 and 21 December 1937 [BMNH, MCZ].

Variation. — In both paratypes the propodeum has some greenish reflections and therefore does not contrast with the head and thorax as much as in the type. Otherwise these females are very similar to the type in color, size, and standard measurements. In both specimens the ocelli are slightly less far removed from the eye margins, OOL being 1.43 and 1.50 x WOT.

Remarks. — This is one of the most brilliantly colored of all bethylid wasps and doubtless the most highly evolved member of this subgenus.

ALPHABETICAL LIST OF ABBREVIATIONS USED IN TEXT

Structures

HE: height of eye (maximum, lateral view)
LFW: length of fore wing

LH: length of head (apical margin of clypeus to median vertex crest)
OOL: ocello-ocular line (minimum distance from eye to lateral ocellus)
WF: width of front (measured at its minimum point)
WH: width of head (maximum, including eyes)
WOT: width of ocellar triangle (including lateral ocelli)

Institutions

AMNH: American Museum of Natural History, New York
ANSP: Academy of Natural Sciences of Philadelphia
BMNH: British Museum (Natural History), London
BSA: Brasil: Secretaria da Agricultura, São Paulo
CAS: California Academy of Sciences, San Francisco
CIS: California Insect Survey, Berkeley
CM: Carnegie Museum, Pittsburgh, Pa.
CU: Cornell University, Ithaca, N.Y.
ENAC: Escuela Nacional de Agricultura, Chapingo, Mexico
HCOU: Hope Collections, Oxford University, England
INHS: Illinois Natural History Survey, Urbana
KU: Kansas University, Lawrence
KSU: Kansas State University, Manhattan
MCZ: Museum of Comparative Zoology, Cambridge, Mass.
UA: University of Arizona, Tucson
UCD: University of California, Davis
USNM: United States National Museum, Washington

LIST OF SPECIES OF *RHABDEPYRIS* OCCURRING IN THE AMERICAS

Subgenus *Rhabdepyris* Kieffer, 1904

1. *mellipes* Evans, n. sp. (♀, Florida)
2. *huachucae* Evans, n. sp. (♀, Arizona)
3. *muesebecki* Evans, n. sp. (♀, ♂, Mexico to Bolivia)
4. *gracilis* Evans, n. sp. (♀, ♂, California; Durango, Mexico)
5. *minutulus* Evans, n. sp. (♀, Peru)
6. *nigriscapus* Evans, n. sp. (♀, Argentina)

Subgenus *Trichotepyris* Kieffer, 1906

Nigropilosus species-group

7. *nigropilosus* Evans, n. sp. (♀, Panama, Brazil)

Megacephalus species-group

8. *megacephalus* (Ashmead), 1893 (♀, ♂, California to Texas)
9. *werneri* Evans, n. sp. (♀, ♂, Arizona)
10. *apache* Evans, n. sp. (♀, ♂, Arizona; Sonora, Mexico)
11. *texanus* Evans, n. sp. (♀, ♂, Texas and Arizona to Morelos, Mexico)
12. *mexicanus* Evans, n. sp. (♀, ♂, Morelos and Chiapas, Mexico)
13. *fortunatus* Evans, n. sp. (♀, Costa Rica)

14. *lupus* Evans, n. sp. (♀, Morelos, Mexico)
15. *carolinianus* Evans, n. sp. (♀, South Carolina, Florida)
16. *subaeneus* Kieffer, 1906 (♀, Nicaragua)
17. *angusticeps* Evans, n. sp. (♀, Arizona)
18. *olivaceus* Evans, n. sp. (♂, Panama, Colombia)
19. *plaumanni* Evans, n. sp. (♀, ♂, Brazil)

Pulchripennis species-group

20. *pulchripennis* Evans, n. sp. (♀, Costa Rica)
21. *iridescens* Evans, n. sp. (♀, Morelos, Mexico)
22. *cupreolus* Evans, n. sp. (♀, Brazil)
23. *amabilis* Fouts, 1927 (♀, ♂, Massachusetts to Florida)

Subgenus *Chlorepyris* Kieffer, 1913

Lobatifrons species-group

24. *luteipennis* Evans, n. sp. (♀, ♂, Brazil to Nicaragua)
25. *lobatifrons* Kieffer, 1910 (♂, Brazil)
    Synonym: *obscuripennis* Kieffer, 1910
26. *septemlineatus* Kieffer, 1906 (♂, Nicaragua, Panama)
27. *quinquelineatus* Kieffer, 1906 (♀, ♂, Mexico to Nicaragua)
28. *nigerrimus* Evans, n. sp. (♀, Bolivia)

Muscarius species-group

29. *muscarius* (Westwood), 1874 (♀, ♂, Mexico to Peru and Brazil)
    Synonym: *microstoma* Kieffer, 1910
30. *puncticeps* Evans, n. sp. (♂, Brazil)
31. *origenus* Kieffer, 1911 (♀, Mexico)
32. *vesculus* Evans, n. sp. (♂, Brazil)
33. *virescens* Evans, n. sp. (♀, ♂, Panama to Peru and Brazil)
34. *viridis* (Cameron), 1888 (♀, Guatemala)
35. *metallicus* Kieffer, 1908 (♀, Nicaragua)

Viridissimus species-group

36. *subviridis* (Kieffer), 1911 (♀, ♂, Mexico to Panama)
37. *blantoni* Evans, n. sp. (♂, Panama)
38. *viridissimus* (Kieffer), 1911 (♀, ♂, Mexico, Guatemala)
    Synonym: *semiviridis* Kieffer, 1913
39. *fulgens* (Brues), 1907 (♀, ♂, Texas to Honduras)
40. *tricolor* Evans, n. sp. (♀, Ecuador)
41. *violaceus* Evans, n. sp. (♀, ♂, Brazil)

(Received May 28, 1964.)

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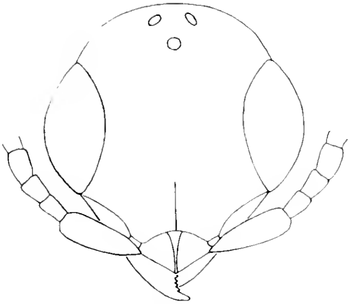
Valid names are printed in italics. Page numbers refer to main references.

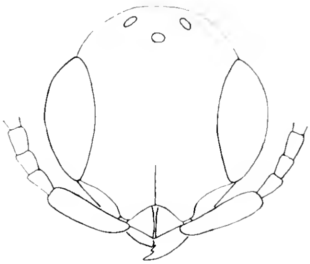
PLATE 1

Heads of female *Rhabdepyris*

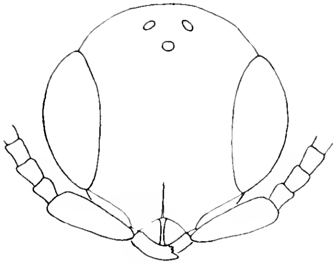
FIG. 1. *R. mellipes* n. sp., type
FIG. 2. *R nigriscapus* n. sp., type
FIG. 3. *R. nigropilosus* n. sp., type
FIG. 4. *R. werneri* n. sp., type
FIG. 5. *R. apache* n. sp., type
FIG. 6. *R. texanus* n. sp., type



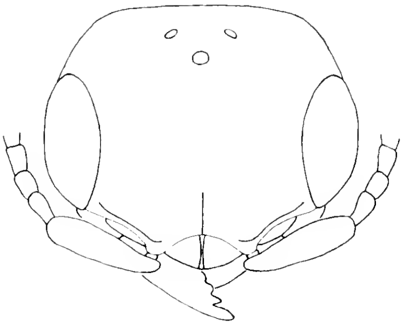
1 mellipes



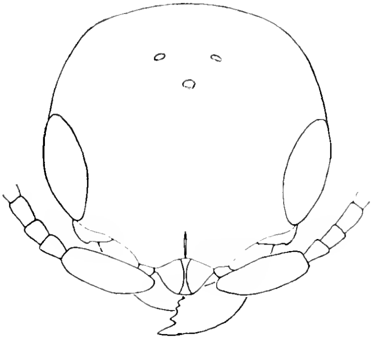
2 nigriscapus



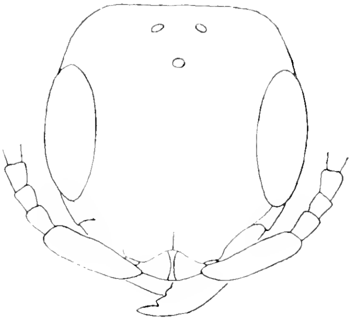
3. nigropilosus



4 werneri



5 apache

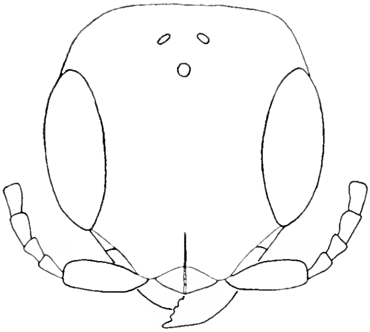


6 texanus

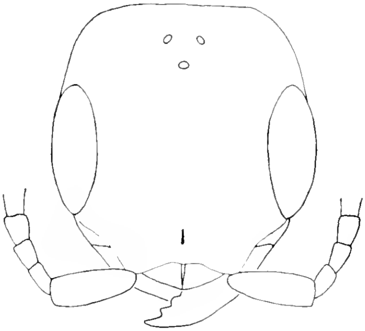
PLATE 2

Heads of female *Rhabdepyris*

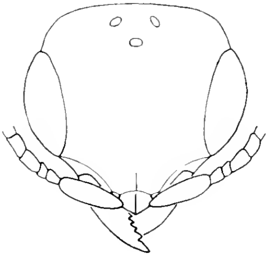
Fig. 7. *R. carolinianus* n. sp., type
Fig. 8. *R. angusticeps* n. sp., type
Fig. 9. *R. fortunatus*, n. sp., type
Fig. 10. *R. iridescens* n. sp., type
Fig. 11. *R. luteipennis* n. sp., type
Fig. 12. *R. nigerrimus* n. sp., type



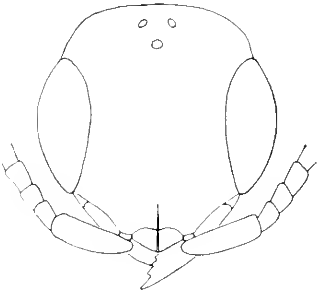
7. caralinianus



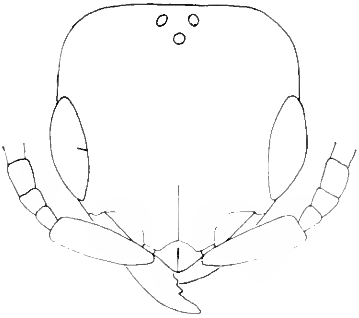
8. angusticeps



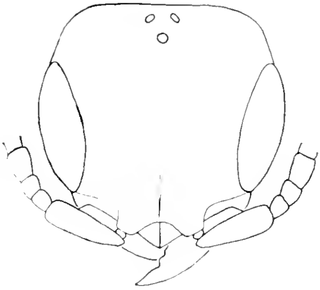
9. fortunatus



10 iridescens



11. luteipennis

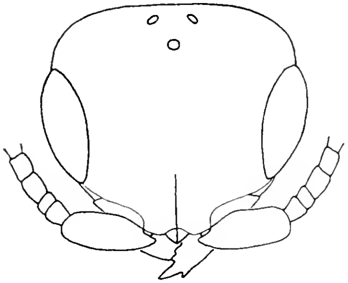


12. nigerrimus

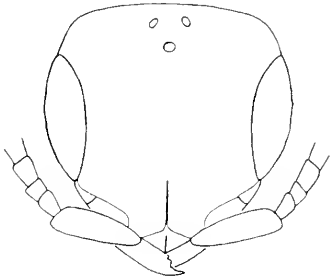
PLATE 3

Heads of *Rhabdepyris* (females and males)

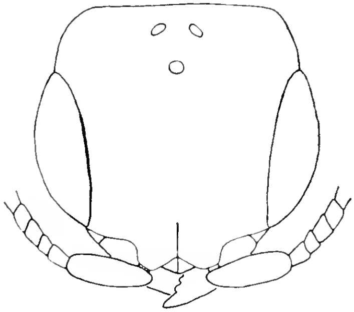
FIG. 13. *R. muscarius* (Westwood), plesiallotype female
FIG. 14. *R. virescens* n. sp., type female
FIG. 15. *R. subviridis* (Kieffer), plesiallotype female
FIG. 16. *R. tricolor* n. sp., type female
FIG. 17. *R. werneri* n. sp., allotype male
FIG. 18. *R. texanus* n. sp., allotype male



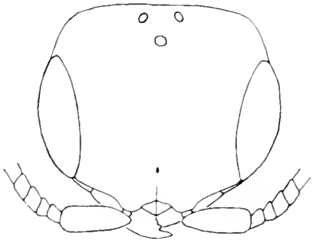
13 muscarius



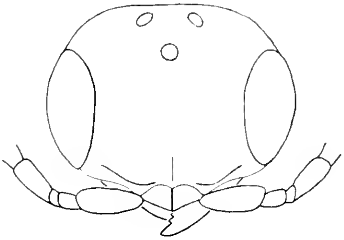
14. virescens



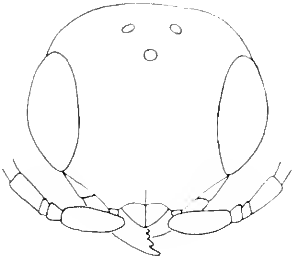
15 subviridis



16. tricolor



17 werneri

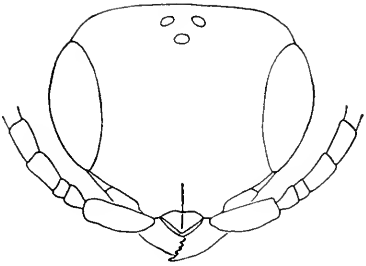


18 texanus

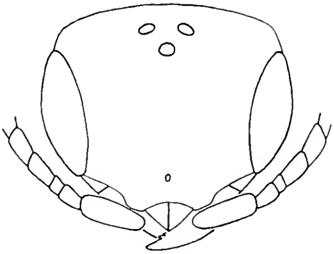
PLATE 4

Heads of male *Rhabdepyris*

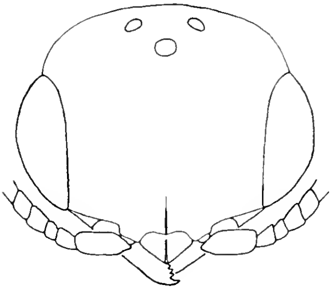
FIG. 19. *R. muscarius* (Westwood), specimen from Chapada, Brazil
FIG. 20. *R. puncticeps* n. sp., type
FIG. 21. *R. virescens* n. sp., allotype
FIG. 22. *R. vesculus* n. sp., type
FIG. 23. *R. blantoni* n. sp., type
FIG. 24. *R. fulgens* (Brues), plesiallotype



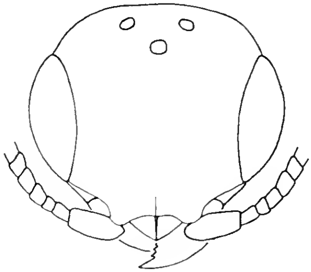
19 muscarius



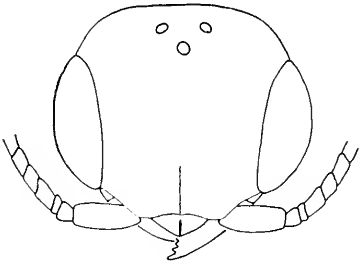
20. puncticeps



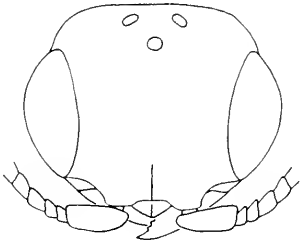
21. virescens



22. vesculus



23. blantoni

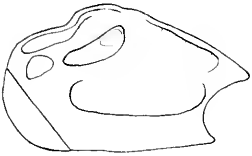


24. fulgens

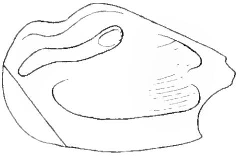
PLATE 5

Mesopleura of female *Rhabdepyris*

Fig. 25. *R. werneri* n. sp., type
Fig. 26. *R. apache* n. sp., type
Fig. 27. *R. texanus* n. sp., type
Fig. 28. *R. carolinianus* n. sp., type
Fig. 29. *R. luteipennis* n. sp., type
Fig. 30. *R. nigerrimus* n. sp., type
Fig. 31. *R. muscarius* (Westwood), plesiallotype
Fig. 32. *R. origenus* Kieffer, type
Fig. 33. *R. virescens* n. sp., type
Fig. 34. *R. subviridis* (Kieffer), plesiallotype
Fig. 35. *R. tricolor* n. sp., type
Fig. 36. *R. violaceus* n. sp., type



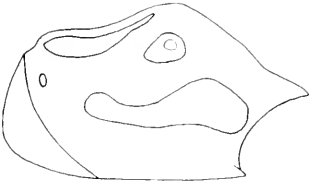
25 werneri



26 apache

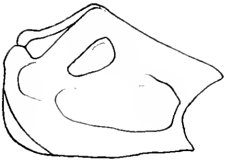
27. texanus

28 carolinianus

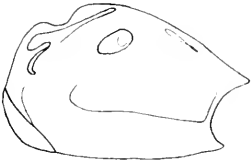


29 luteipennis

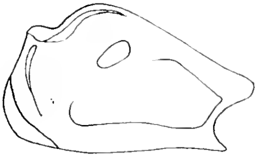
30. nigerrimus



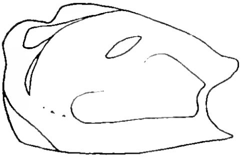
31. muscarius



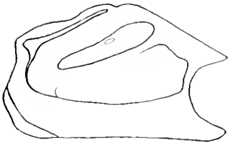
32. origenus



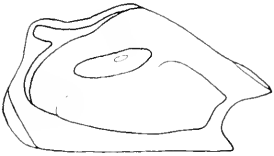
33 virescens



34. subviridis



35. tricolor



36 violaceus

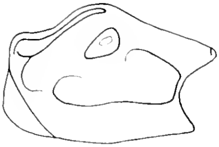
PLATE 6

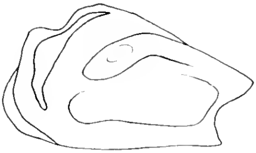
Mesopleura of male *Rhabdepyris*

FIG. 37. *R. muscarius* (Westwood), specimen from Chapada, Brazil
FIG. 38. *R. vesculus* n. sp., type
FIG. 39. *R. virescens* n. sp., allotype
FIG. 40. *R. blantoni* n. sp., type
FIG. 41. *R. viridissimus* (Kieffer), type
FIG. 42. *R. fulgens* (Brues), plesiallotype

Mandibles of female *Rhabdepyris*

FIG. 43. *R. megacephalus* (Ashmead), type
FIG. 44. *R. werneri* n. sp., type
FIG. 45. *R. fortunatus* n. sp., type
FIG. 46. *R. carolinianus* n. sp., type
FIG. 47. *R. subaeneus* Kieffer, type
FIG. 48. *R. angusticeps* n. sp., type
FIG. 49. *R. luteipennis* n. sp., type
FIG. 50. *R. muscarius* (Westwood), plesiallotype
FIG. 51. *R. virescens* n. sp., type
FIG. 52. *R. subviridis* (Kieffer), plesiallotype
FIG. 53. *R. viridissimus* (Kieffer), plesiallotype
FIG. 54. *R. fulgens* (Brues), type


37 muscarius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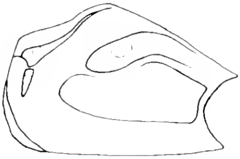
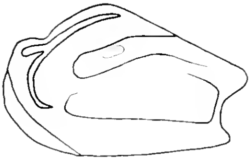
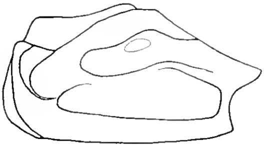
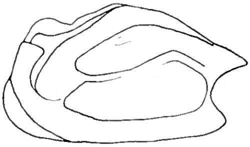
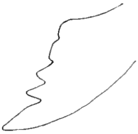

39 virescens


40 blantoni


41 viridissimus


42 fulgens

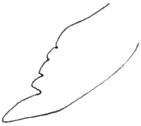

43 megacephalus


44 werneri


45 fortunatus

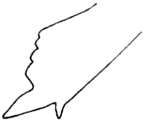

46. carolinianus


47 suboeneus

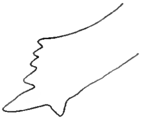

48 angusticeps


49. luteipennis


50. muscarius


51. virescens


52. subviridis


53. viridissimus

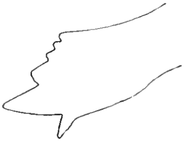

54 fulgens

PLATE 7

Claws of posterior tarsi of *Rhabdepyris*

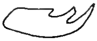
Fig. 55. *R. luteipennis* n. sp., type female
Fig. 56. *R. luteipennis* n. sp., allotype male
Fig. 57. *R. quinquelineatus* Kieffer, type female
Fig. 58. *R. nigerrimus* n. sp., type female
Fig. 59. *R. muscarius* (Westwood), plesiallotype female
Fig. 60. *R. muscarius* (Westwood), type male
Fig. 61. *R. vesculus* n. sp., type male
Fig. 62. *R. virescens* n. sp., type female
Fig. 63. *R. virescens* n. sp., allotype male
Fig. 64. *R. blantoni* n. sp., type male
Fig. 65. *R. subviridis* (Kieffer), type male
Fig. 66. *R. viridissimus* (Kieffer), plesiallotype female
Fig. 67. *R. viridissimus* (Kieffer), type male
Fig. 68. *R. fulgens* (Brues), type female
Fig. 69. *R. violaceus* n. sp., type female
Fig. 70. *R. violaceus* n. sp., allotype male

Basal segments of antennae

Fig. 71. *R. luteipennis* n. sp., allotype male
Fig. 72. *R. quinquelineatus* Kieffer, plesiallotype male
Fig. 73. *R. subviridis* (Kieffer), type male
Fig. 74. *R. fulgens* (Brues), type female

55. luteipennis ♀

56. luteipennis ♂



57. quinquelineatus ♀

58 nigerrimus ♀

59. muscarius ♀

60. muscarius ♂

61. vesculus ♂

62. virescens ♀

63. virescens ♂

64 blantoni ♂

65. subviridis ♂

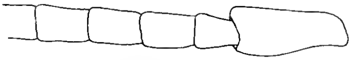
66. viridissimus ♀

67. viridissimus ♂

68. fulgens ♀

69. violaceus ♀

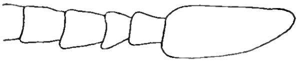
70. violaceus ♂



71 luteipennis ♂

72. quinquelineatus ♂

73. subviridis ♂



74. fulgens ♀

Bulletin of the Museum of Comparative Zoology
HARVARD UNIVERSITY
Vol. 133, No. 3

NELDASAURUS WRIGHTAE, A NEW RHACHITOMOUS LABYRINTHODONT FROM THE TEXAS LOWER PERMIAN

By John Newland Chase
Ohio Wesleyan University, Delaware, Ohio

With Five Plates

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
June 25, 1965

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Bull. Mus. Comp. Zool., Harvard Univ., **133**(3): 153-225, June, 1965

No. 3. NELDASAURUS WRIGHTAE, *A New Rhachitomous Labyrinthodont from the Texas Lower Permian*[1]

By JOHN NEWLAND CHASE
Department of Zoology,
Ohio Wesleyan University, Delaware, Ohio

TABLE OF CONTENTS

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[1] This paper is part of a thesis submitted to the Department of Biology of Harvard University as partial fulfillment of the requirements for the degree of Doctor of Philosophy, August, 1962.

INTRODUCTION

Since their discovery in 1875, the Lower Permian redbeds of north central Texas have been an important source of fossil vertebrates. Until recent decades, however, the fauna of this region (mainly described by Cope, Case, and Williston) was derived from a very limited series of horizons, which include the upper portions of the Wichita Group and the lowest part of the overlying Clear Fork. Collections made in the uppermost beds of the Clear Fork by Olson (1948, 1951 a-c, 1955) and in the Lower Wichita formations by Romer and associates (Romer, 1935, 1947, 1958) have extended our knowledge and given us some concept of the faunal assemblages that preceded and followed those of the typical Lower Permian faunas. This paper is concerned with certain amphibian remains recovered from the lower levels of the Wichita.

A number of expeditions from the Museum of Comparative Zoology at Harvard College have been made to the Texas redbeds from 1934 onward. In most cases these had the special objective of obtaining remains from the lower horizons of the Wichita Group—the Putnam, Moran and Pueblo formations in descending order. The finds have included numerous identifiable amphibian specimens (mainly from the Putnam and Moran) which, for the most part, pertain to genera already well known from the higher, "classic," Wichita formations, the Admiral and the Belle Plains. These include such forms as *Trimerorhachis, Eryops, Broiliellus, Tersomius, Parioxys* and *Acheloma.* However, the lower formations showed indication of a somewhat different and more primitive faunal assemblage, particularly in the occurrence of the primitive rhachitome, *Edops* (Romer and Witter, 1942).

A further indication of the faunal difference between the upper, typical, Wichita and the lower Wichita formations was the recovery in the earlier trips to these lower beds of remains of an obviously new rhachitome too fragmentary to permit adequate description. Vertebral and limb materials showed some similarity to *Trimerorhachis,* a form not identified with certainty below the Putnam (Olson, 1955), but such skull remains as were recovered indicated a narrow, attenuated snout quite different from that of *Trimerorhachis.*

A collecting trip from the Museum of Comparative Zoology in 1954 under the direction of Dr. Alfred S. Romer resulted in the recovery of a nearly complete skull of this problematical form, with attached lower jaws and some postcranial material in a common block. The certain association of the skull with postcranial materials made possible for the first time a comprehensive description of this new form and the assignment of the specimens in previous collections to a new genus.

The fossil material described in this paper is assigned to a new genus and species of rhachitomous labyrinthodont for which I propose the name *Neldasaurus wrightae*. Both generic and specific designations are in honor of Miss Nelda E. Wright, Research Assistant and Editor of Publications of the Museum of Comparative Zoology, who discovered the holotype specimen.

ACKNOWLEDGEMENTS

My appreciation is due to several persons whose aid I rereceived during the course of this study. I should like first to express my sincere thanks to Dr. Alfred S. Romer, under whose inspiring direction this work was undertaken and whose continued interest and advice have been of invaluable assistance. I am indebted to Dr. Donald Baird of Princeton for many helpful suggestions and permission to use his information on the Linton fauna; to Dr. Nicholas Hotton III of the United States National Museum for information on *Acroplous vorax;* to Dr. Edwin H. Colbert of the American Museum of Natural History for access to specimens of *Trimerorhachis;* to Dr. Craig C. Black of the Carnegie Museum for the loan of specimens; to Dr. Robert Carroll then at the Museum of Comparative Zoology for information pertaining to early edopsoids; to Dr. Carl Gans of the University of Buffalo and Mr. Frank White of the Biological Laboratories at Harvard for assistance in taking photographs of the specimens. Thanks are also due to Mr. Arnold Lewis of the Museum of Comparative Zoology at Harvard, who gave freely of his time and knowledge in introducing me to the techniques of fossil preparation. Thanks are due also to Dr. Ernest E. Williams and Professor Bryan Patterson of the Museum of Comparative Zoology for critical reading of the manuscript. I am indebted to Miss Nelda Wright for many valuable suggestions during the preparation of this paper.

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SYSTEMATIC DESCRIPTION[1]

Class AMPHIBIA
Order TEMNOSPONDYLI
Suborder RHACHITOMI
Superfamily TRIMERORHACHOIDEA
Family TRIMERORHACHIDAE
NELDASAURUS, gen. n.

Type species. Neldasaurus wrightae sp.n.

Generic Diagnosis. — A low-skulled labyrinthodont amphibian which closely resembles *Trimerorhachis* in size, many skull proportions, body and limbs, dermal roof pattern, and palate. *Neldasaurus* differs from *Trimerorhachis* in the following respects: orbits midway between snout and occiput; snout narrow; lacrimal elongate but not reaching the external naris; nasals, prefrontals and frontals elongate; external nares close together, their long axes more or less parallel; jugal entering the orbital border; prevomers elongate and the choanae broadly separated from the anterior border of the interpterygoid vacuities; larger number of teeth than in *Trimerorhachis* in the lower jaw and the marginal series of the upper jaw; a tusk pair on the ectopterygoid; a foramen in the lower jaw for the reception of vomerine tusks; opisthotic and prootic unossified; pleurocentra as high as the intercentra; clavicles meeting in front of the interclavicle.

NELDASAURUS WRIGHTAE sp. n.

Holotype. — MCZ 2200, including a nearly complete skull and attached lower jaws, central and neural arch vertebral elements, a partial pectoral girdle, limb bones and remnants of dermal armor.

Type Locality and Horizon. — Terrapin School, Section A-1266, BBB + CRR Survey, Archer County, Texas; Moran Formation, Wichita Group, Permian. Collected by A. S. Romer party, 1954.

Diagnosis. — As for genus.

Referred Specimens. — MCZ Nos. 1371, 1381, 1438, 1463, 2404, 2406, 2407, 2516, 2518, 2519.

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[1] The classification used here follows Romer (1947).

DESCRIPTIVE LIST OF MATERIALS

The material consists of the holotype and the following specimens, all from the Wichita Group of the Texas Lower Permian.

MCZ 1371. A partial skull and left lower jaw, dorsal vertebrae — some in articulated series, ribs, a partial clavicle and interclavicle, a nearly complete forelimb, dermal scales and armor. There is also what appears to be a pelycosaur foot bone. Putnam Formation, Table Branch, South Fork of the Little Wichita River, G. W. Stell Survey, Section A-382, 10 miles west of Anarene in Archer County. Collected by R. V. Witter party, 1936.

MCZ 1381. Fragmentary remains of several small individuals. Same data as for MCZ 1371.

MCZ 1438. Poorly preserved remains of skulls and postcranial materials of at least two individuals of little use for purposes of description. Putnam Formation, 1 mile west of Archer City in the Archer City bone bed, Section 151, American Tribune New Colony Subdivision, southwest part Archer County. Collected by R. V. Witter party, 1936.

MCZ 1463. Fragmentary cranial and postcranial materials in a limey nodule. Section 16, Falls County School Land, Archer County, about 7 miles southwest of Anarene. Collected by R. V. Witter party, 1936. The formation is either Putnam or Moran.

MCZ 2404. Fragmentary portions of lower jaw and postcranial materials. Moran formation at Terrapin School, BBB + CRR Survey, A-1266 in southern Archer County. Collected by A. S. Romer party, 1950.

MCZ 2406. A large number of discrete skull and postcranial materials, mostly fragmentary, including the proximal ends of a humerus and a femur. There is also a *Trimerorhachis*-like intercentrum, a complete ring central element and scraps of a larger labyrinthodont. Moran Formation near Padgett in the northeast part of William Tryndale Survey, Young County. Collected by A. S. Romer, 1942.

MCZ 2407. Fragmentary vertebral materials, the distal ends of a radius and a femur and portions of a pterygoid. Collection site as for MCZ 2406. Collected by R. V. Witter, 1942.

MCZ 2516. Separate and disarticulated elements, mostly incomplete; including parts of a lower jaw, a right femur, an ilium, and vertebrae. Moran Formation, ¾ mile north and 1 mile west of Padgett Schoolhouse, Young County. Collected by R. V. Witter party, 1936.

MCZ 2518. Fragmentary skull and jaw materials, numerous partial vertebral elements, ribs, pectoral plates and two ilia, probably all pertaining to one individual. Moran Formation in Padgett, the northwest part of the William Tryndale Survey, MCZ Field No. 9, Young County. Collected by A. S. Romer, 1951.

MCZ 2519. A partial intercentrum. Moran Formation west of Cottonwood Creek, about Section 48, County School Land, Archer County. Collected by A. S. Romer, 1954.

ANATOMICAL DESCRIPTION OF GENUS AND SPECIES

General Skull Morphology

Of the three principal skull specimens, the holotype, MCZ 2200 (Pls. 1 and 2), is the most complete. The figures and description are primarily based on this specimen, but supplementary information was obtained from MCZ 1371 (Pl. 3), MCZ 1438 (Pl. 4), and also the fragments included in MCZ 2518. The holotype skull is described first.

The dermal roof, although fairly complete, is displaced to the left in relation to the palate and has been subjected to post-mortem crushing so that the skull appears to have retained its original depth only in the right suborbital region. Horizontal pressures have caused some overlapping of the medial boundaries of the central dermal bones.

Intrusion of the articular portions of the lower jaws from below partially obscures the relationships of the quadrate region. The anterior extremity of the snout is incomplete in all of the specimens, but the portions that remain permit a reasonable restoration. The right lower jaw of the holotype has retained a fairly normal position throughout much of its length so that most of the lateral skull margin is visible. However, the posterior quarter of the ventrolateral border of the skull roof has been damaged and details of structure are hard to trace.

Post-mortem flattening of the skull and damage to the skull margins introduce some uncertainty in the determination of cranial dimensions. However, the figures obtained from the reconstructed skull roof, the palate and the lower jaw, give the general dimensions, as set forth in Table 1, with a fair degree of accuracy. Determination of the depth of the skull was based primarily on the transverse dimensions of the palate and the resultant restoration of the skull roof to fit these dimensions.

The skull (Figs. 1, 2, 3 and 5) is of moderate size. The snout is narrow but bluntly rounded anteriorly, the skull increasing in breadth toward the back, having its greatest width in the occipital region. Allowing for a slight backward projection of the condyle from the occipital border, the suspensorium is about 1.5 cm behind the level of the condyle. However, the otic notch is not as highly developed as in *Trimerorhachis,* and the contour of the central posterior rim of the skull table is less concave than it is in that animal.

The occiput slopes downward and backward at an angle of approximately 23° from the vertical in the preserved skull. But, though some degree of slope may be normal, the occiput may have been more nearly vertical in life.

The depth of the skull midway between the orbits and the end of the snout is approximately 13 mm, and the height of the cheek below the orbit is 14 mm. The height of the occiput is about 39 mm. Thus, the depth of the skull increases from front to back, the increase being considerably more pronounced in the postorbital region, the snout being generally flattened.

Determination of the original skull roof topography is difficult because of post-mortem distortion. The evidence seems to indicate a more or less flat or slightly concave surface in the central region of the skull table bounded by a low ridge on each side which runs from the tabular to the outer posterior corner of the orbit. The outer face of the ridge slopes gently downward, becoming confluent with the cheek, and the inner face dips down to the central region of the skull table.

The mid-orbit to snout length is approximately 49.3 per cent of the midline skull length. The dorsally directed orbits are oval in shape and somewhat smaller in relation to overall skull size than those of *Trimerorhachis*[1], though, as in *Trimerorhachis,* the interorbital space is narrow. The inner border of the orbit is slightly elevated above the surface of the skull roof, the smooth, medial margin having a depth of 3 mm. The rest of the margin, which shows no appreciable elevation, is not as thick.

A small parietal foramen is present in the midline between the parietals, 2.9 cm behind the posterior orbital border. The distance from the orbit to the parietal foramen is equal to 38 per cent of the skull table length, a shorter distance than that seen in *Trimerorhachis,* where the comparable figure is 50 per cent.

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[1] This comparison is based on the ratio of skull width × skull length/orbit width × orbit length.

In agreement with the dimensions of the rostrum, the external nares are not as widely separated as they are in other trimerorhachoids. The medial margin of the naris is slightly elevated above the surface of the internarial region, and the opening is somewhat constricted in its posterior third. The lateral border of the naris is separated from the skull margin by a dorsal exposure of the premaxilla and the maxilla of approximately 5.5 mm.

Skull MCZ 1371 (Pl. 3) exhibits overall dimensions that are closely comparable to those of the holotype, and the dimensions given in Table 1 can be accepted with a fair degree of certainty. Extreme flattening makes the determination of skull height difficult, but it appears to agree closely with that of MCZ 2200.

The preserved portions of skull MCZ 1438 (Pl. 4) appear to represent a somewhat larger animal than the preceding forms. Overall length cannot be determined, but the dimensions of the preorbital region suggest proportions similar to those of MCZ 2200 and 1371.

The dermal roof bones of MCZ 2518 are disarticulated and incomplete so that comparison of general dimensions of this specimen and the others is impossible.

TABLE I

Measurements (in mm) of Dermal Skull Roof

	MCZ No. 2200	MCZ No. 1371	MCZ No. 1438
Length			
Snout to end of skull table	158	—	—
Snout to quadrate	173	174	—
Snout to mid-orbit	78	80	86
Orbit	20	20 (est.)	—
External naris	13	—	14
Width			
Snout behind naris	40	42	46
Orbital region	70	74	—
Quadrate level	120	—	—
Orbit	16	15 (est.)	—
External naris	8	—	8
Internarial	10	—	12
Height			
Mid-rostral	13	—	13 (est.)
Suborbital	14	14 (est.)	15 (est.)
Occiput	39	—	—

BONES OF THE DERMAL SKULL ROOF

(Figures 1 and 2)

Some sutures on one or another of the skull specimens, MCZ 2200, 1371, 1438, 2418, were readily traced, but the location of others, which were not recognizable per se, was based on the sculpture patterns of individual bones. Centers of ossification were determined by considering their relationship to the sensory canal system, which is typically associated with the center of growth in each bone (Bystrow, 1935; Westoll, 1943; Parrington, 1949). I believe that the general pattern of the skull roof of MCZ 2200, as figured, is reasonably accurate.

The dermal roof pattern closely resembles that of *Trimerorhachis.* Differences in the shape of individual bones in the two animals are obviously due in large measure to the differences in skull proportions mentioned above.

The dermal bones of the skull roof are treated here as comprising four groups: (1) the paired elements of the dorsal midline, (2) the circumorbital bones, (3) the bones of the temporal region that form the lateral margin of the skull table, and (4) the marginal tooth-bearing bones and the cheek bones.

(1) The nasals are long, roughly rectangular bones which extend more than half the distance from the naris to the orbit, their shape sharply contrasted to the squarish nasals in *Trimerorhachis.*

The elongate frontals, with over half their length extending into the preorbital region are also in contrast to conditions in *Trimerorhachis,* in which form the nasals make a much greater contribution to the midfacial area than do the frontals.

The parietals form most of the central portion of the skull table, extending from the posterior border of the frontals to the postparietal suture. A parietal opening of modest size is located centrally between them.

The roughly pentagonal postparietals are relatively small bones. Posteriorly, they turn down over the rim of the skull table in an occipital exposure. A stout occipital flange of the postparietal, which rests on a dorsal extension of the exoccipital, bounds the supraoccipital region laterally and forms the medial rim of the posttemporal fenestra (Fig. 5). The tabular does not appear to take part in the formation of the descending flange.

(2) The circumorbital series, including the prefrontal, postfrontal, postorbital, jugal, and lacrimal, is complete.

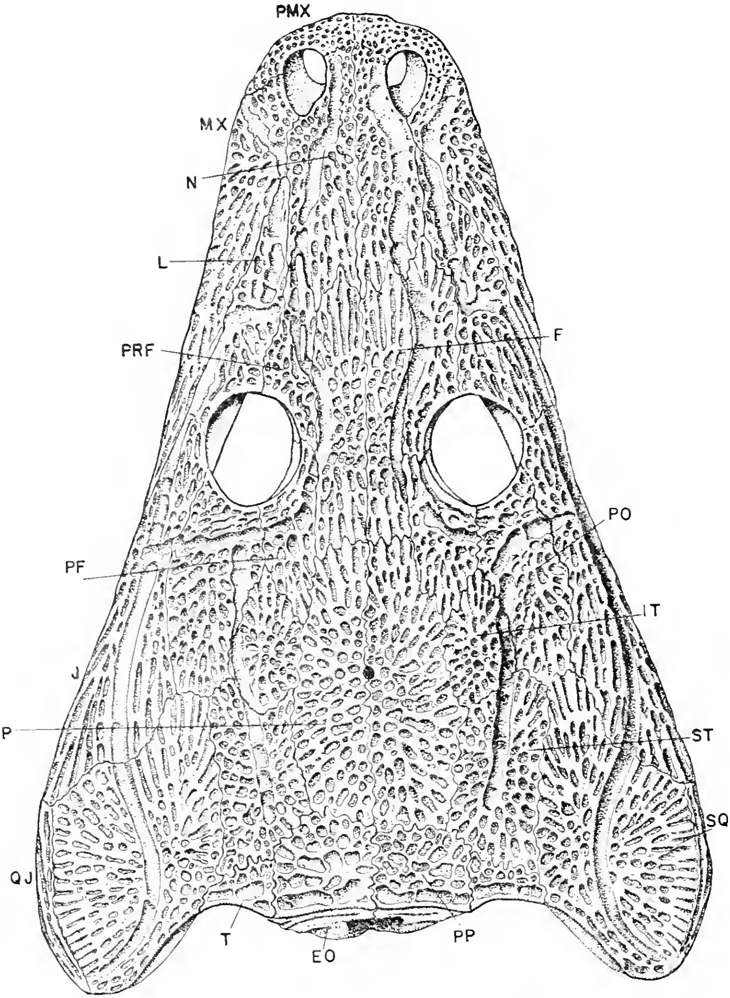

FIG. 1. Dorsal view of skull roof of *Neldasaurus wrightae,* n. gen., n. sp., restored, × .75. Portions of the sensory canal grooves and some sutures on the right have been restored to agree with conditions on the left. Abbreviations: EO, exoccipital; F, frontal; IT, intertemporal; J, jugal; L, lacrimal; MX, maxilla; N, nasal; P, parietal; PF, postfrontal; PMX, premaxilla; PO, postorbital; PP, postparietal; PRF, prefrontal; QJ, quadratojugal; SQ, squamosal; ST, supratemporal; T, tabular.

The prefrontal is a narrow bone which forms the anteromedial margin of the orbit, ending halfway back on the medial rim.

The postfrontal is narrow anteriorly where it joins the prefrontal to complete the medial rim of the orbit. Behind the orbit it becomes somewhat wider.

The jugal is a large bone approximately 7 cm long, and the longest skull roof bone, aside from the maxilla. Unfortunately, the suborbital region in all of the specimens is poorly preserved or damaged, but a break in the surface contour of the right cheek below the orbit in MCZ 2200 and the pattern of the sculpture in this area suggest that there was a lacrimal-jugal suture about halfway back on the lateral rim of the orbit. If this interpretation is correct, the jugal forms at least a small part of the orbital border.

The postorbital forms most of the posterior orbital rim, meeting the jugal laterally on the outer margin of the orbit, though the exact position of the suture is not known.

The lacrimal is elongate. It forms much of the anterolateral rim of the orbit and, though it fails to reach the naris, it extends four-fifths of the distance from the orbit to the naris in the holotype skull.

(3) Primitively, the lateral margin of the skull table includes an intertemporal bone as well as supratemporal and tabular. The posterior limits of the intertemporal, a relatively small bone here, were difficult to trace but the anterior and medial boundaries were well defined on MCZ 2200 and MCZ 2518.

The tabular is the smallest bone in the skull table. Laterally it has a short contact with the squamosal, excluding the supratemporal from the margin of the otic notch, a feature which tends to accompany modest development of the latter (Romer, 1947, p. 24). Medially, where it meets the postparietal, the tabular forms most of the dorsal margin of the posttemporal fossa. Midway in its posterior border the tabular has a ventral projection, near the inner edge of the otic notch, which is the posterior end of a low ridge that continues anteriorly under the skull roof for a distance of 7 mm. The depth of this ridge, or flange, is approximately 3 mm.[1]

Immediately anterior to its posterior border the ventral surface of the tabular is excavated so that a depression is formed,

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[1] Case (1935) mentions a "low rugose line" running forward and inward on the under surface of the tabular from the inner edge of the otic notch in his *Trimerorhachis* specimen 16002, which may be comparable to the structure described here.

bounded medially by the "flange" described above and posteriorly by the posterior rim of the tabular. Laterally this fossa, which is about 9 mm wide, is bounded by a ventrally-directed process from the posteromedial edge of the squamosal. Little of the underside of the skull roof of this region can be seen and its precise character, partially visible only in the holotype, is difficult to interpret because of its imperfect condition.

(4) The boundaries of the marginal tooth-bearing bones, the premaxilla and maxilla, were hard to find in the rostral region. Their outlines as finally determined are a composite of the patterns that could be seen on parts of four specimens, MCZ 2200, 1371, 1438, and 2518. The premaxilla, seen best in MCZ 1438, apparently had a small dorsal exposure anteriorly, separating the anterior rim of the external naris from the rostral border by a distance of approximately 3 mm. The union of the premaxilla with the nasal posteriorly appears to have been close to the anterior narial rim on the medial side. Medially, the premaxilla joins its fellow of the opposite side, and posteriorly, lateral to the naris, it joins the maxilla near the middle of the lateral rim of the naris.

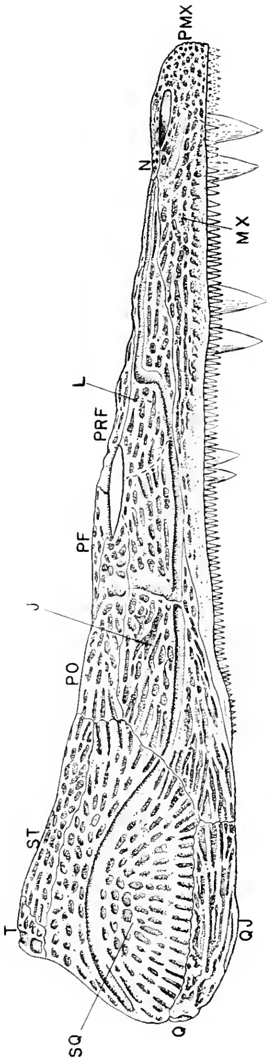

FIG. 2. Skull of *Neldasaurus wrightae,* in lateral aspect. Restored, × .75. Abbreviation: Q, quadrate. Other abbreviations as in Figure 1.

The maxilla extends along the lateral margin of the skull for about two-thirds of the skull length, its dorsal exposure dwindling rapidly towards the rear. Posteriorly, it comes close to the quadratojugal. Conditions here are uncertain, but the jugal appears to enter the skull margin for a short distance between the maxilla and quadratojugal.

The postorbital cheek region is formed in typical fashion by the squamosal and quadratojugal. Posteriorly the squamosal has a contact with the anterior portion of the quadrate and forms part of the outer margin of the otic notch. On the inner posterior margin of the cheek it has a ventral and anteriorly directed process, about 6 mm deep, which joins the quadrate ramus of the pterygoid on its lateral edge.

The quadratojugal forms the posterolateral margin of the skull below the squamosal. Conditions in the left quadrate region of MCZ 2200, as near as can be determined, are like those in MCZ 1371, where it is better preserved. The posterior edge of the quadratojugal, forming a shallow, concave rim, is separated from the lateral margin by a sharp angle. The inner posterior end of the bone forms a medial projection posterior to the sutural surface for the squamosal. The posterior rim of this medial process probably formed part of the border of the quadrate foramen. The sutural face on the quadratojugal for articulation with the squamosal, therefore, does not reach the anterior edge of the foramen, and the squamosal does not reach its border. The remainder of the border of the quadrate foramen was apparently formed by the quadrate. Conditions here appear to be comparable to those seen in *Trimerorhachis* (Case, 1935, fig. 4; Williston, 1915, fig. 3).

The pattern of the dermal roof bones of MCZ 1371 (Pl. 3) appears to be identical to that of the holotype. This specimen offers further evidence of the relations of the lacrimal, which is here prevented from reaching the posterior narial border by a union of the maxilla and the nasal. Also, although the situation is not entirely clear, the lacrimal appears to have a stout union with the jugal below the orbit so that the jugal forms more than half of the lateral orbital border.

The skull roof of MCZ 1438 (Pl. 4) is incomplete, but it appears to follow the general pattern seen in MCZ 2200 and 1371. In contrast to its form in the other skulls, the lacrimal here reaches to, or nearly to, the external naris. The only other apparent difference is in the slightly larger dimensions of the individual bones, which agree with the general porportions of the skull.

As stated earlier, the skull roof of MCZ 2518 consists of a number of isolated fragments. In so far as it can be traced, the dermal roof pattern is like that of the holotype.

The sculpture of the dermal roof bones consists of ridges and pits, or grooves, radiating from a center of ossification in each bone. Notable differences between the sculpture pattern in *Neldasaurus* and *Trimerorhachis* are obviously correlated with differences in the shape of individual bones in the two animals. As any figure shows (Bystrow, 1938, fig. 11), there is no linear sculpture in *Trimerorhachis,* whereas in *Neldasaurus* there is a suggestion of linear sculpture on adjacent regions of the frontals and nasals and on the frontals and parietals. The sculpture also tends to become linear in portions of other long bones in *Neldasaurus* such as the lacrimal and jugal.

The Sensory Canal System

The channels of a sensory canal system are well defined on the surface of the dermal roof bones in *Neldasaurus* (Figs. 1 and 2). In all the specimens the pattern of these channels is remarkably constant, and, except for the anterior rostral portions of the supraorbital and infraorbital channels, the pattern is clear.

The pattern of the sensory canal system generally resembles that of *Trimerorhachis* (Case, 1935, fig. 5 A) but differs in some particulars. In *Neldasaurus* the supraorbital groove crosses the postfrontal, prefrontal, and nasal but does not enter the lacrimal as in *Trimerorhachis.* The anterior portion of the infraorbital groove in *Neldasaurus* runs from the jugal along the suture between the maxilla and lacrimal, then continues for some distance on the lacrimal. The anterior portion of the infraorbital groove in *Trimerorhachis* is confined to the maxilla except for a short loop onto the lacrimal.

The position of the temporal groove in *Neldasaurus* is esssentially as in *Trimerorhachis,* though it is slightly more medial in *Neldasaurus.* A jugal sulcus of the sensory canal system, separated by a short gap from the infraorbital groove on the jugal, crosses the jugal-squamosal suture near its midpoint and has the shape of a medially convex curve on the central region of the squamosal, swinging laterally near the posterior margin to end at the posterolateral corner of the bone. It does not appear to have passed across the quadratojugal, but over the posterior border of the squamosal, just behind the end of the quadratojugal, to its connection with the lower jaw system. This groove is unknown in *Trimerorhachis.*

The courses traced by the sensory canal grooves of MCZ 1371, 1438 and 2518, where they can be seen, are the same as those on the holotype.

PALATE AND PALATOQUADRATE

(Figure 3 and Plate 2)

In all of the skull specimens the lower jaws lay in more or less normal closed position against the ventral surface of the skull, thus obscuring the lateral palatal surface. Fortunately, it was possible to expose this region by removing the right lower jaw ramus and 2.5 cm of the anterior end of the left jaw ramus from the ventral surface of the holotype skull. The description and reconstruction of the palate and the ventral skull surface, as shown in Figure 3, were mainly based on this specimen. Restored portions are hatched in the figure.

The general form and proportions of the central and posterior portions of the palate in *Neldasaurus,* including the presence of large interpterygoid vacuities, resemble conditions in *Trimerorhachis.* However, the region of the palate in front of the interpterygoid vacuities in *Neldasaurus,* reflecting the proportions of the elongate snout, is more extensive.

The anterior end of the palate is incomplete, but the evidence suggests that the premaxilla had a moderate palatal exposure. The ventral exposure of the maxilla, throughout most of its length, represents little more than the width of the tooth row.

The maxilla accounts for nearly two-thirds of the lateral margin; its posterior end briefly enters the anterior portion of the lateral rim of the subtemporal fossa. The jugal apparently enters for a short distance into the ventral margin of the skull posterior to the maxilla, but most of the lateral border of the fossa is formed by the quadratojugal.

Determination of the extent of the palatal exposure of the maxilla adjacent to the internal naris was difficult, and some uncertainty exists. Since the palatine appears to form most if not all of the lateral border of the choana, the maxilla could enter

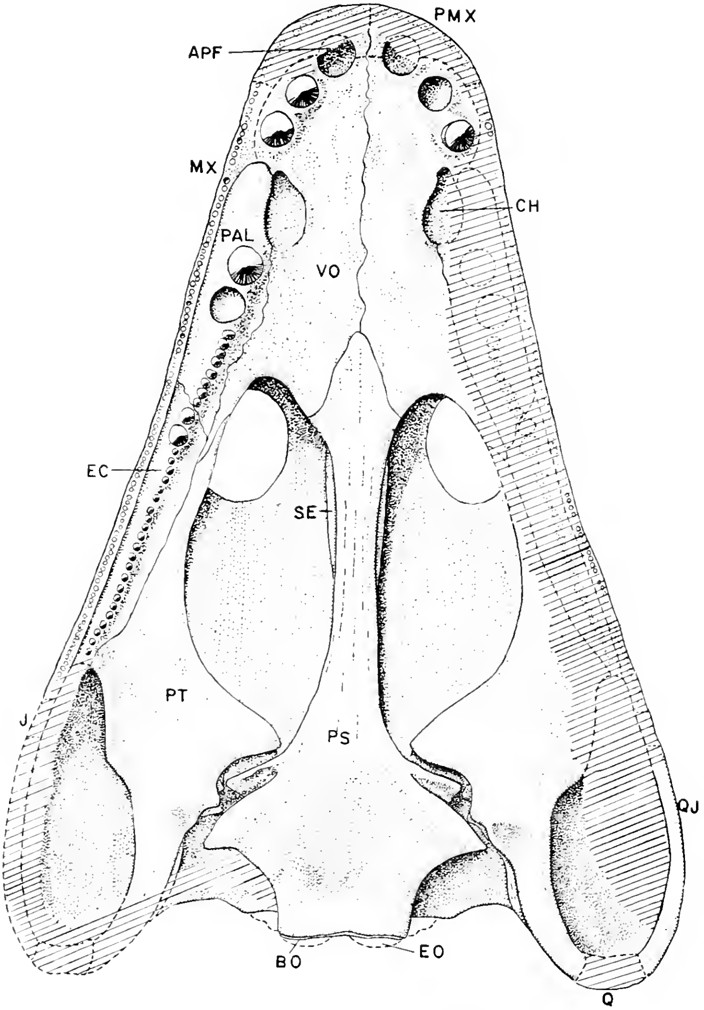

FIG. 3. Reconstruction of skull of *Neldasaurus wrightae* in palatal aspect, × .75. Restored areas are hatched. Abbreviations: APF, anterior palatal fenestra; BO, basioccipital; CH, choana; EC, ectopterygoid; EO, exoccipital; J, jugal; MX, maxilla; PAL, palatine; PMX, premaxilla; PS, parasphenoid; PT, pterygoid; Q, quadrate; QJ, quadratojugal; SE, sphenethmoid; VO, vomer.

its border (if at all) only at the outer anterior corner. Exclusion of the maxilla from the lateral rim of the choana by a union of the vomer and the palatine, which appears to be the case here, is to my knowledge reported in only one other form, *Eobrachyops townendi* (Watson, 1956). The suture between the maxilla and premaxilla can not be seen in ventral aspect. Nevertheless, on the basis of its location on the lateral skull margin, it probably lies close to the level of the anterior member of the vomerine tusk pair.

The marginal teeth are small, crowded and numerous. By counting the teeth in areas where they can be seen, it was possible to estimate a total number of 93 maxillary teeth. The anterior teeth are less than 1 mm in diameter, and in the anterior portion of the maxilla there are slightly less than 10 teeth per cm, while towards the posterior end, where the teeth are still smaller, there are approximately 11 per cm. The length of the tooth-bearing margin of the premaxilla, as reconstructed, is approximately 2.5 cm. The narrow palatal exposure of this bone suggests small tooth size in this region also and, allowing for some decrease in the number of teeth per unit area, the premaxilla should have held at least 15 teeth. In some regions of the maxilla it was noted that teeth alternated with replacement sockets, though no consistent pattern could be seen.

Although the anterior portion of the palate in MCZ 2200 is damaged, there is evidence of the presence of two sets of openings, the anterior palatine fenestrae and the choanae. Immediately anterior, and slightly medial, to the anterior vomerine tusk on each side there is an opening in the palate. In the matrix deposited in this region, on both sides, there are remnants of the upper ends of symphysial tusks belonging to the lower jaw. It appears that anterior palatal fenestrae were present on the suture between the premaxillae and the vomers in *Neldasaurus*. The matrix-filled space containing the upper end of the tusk is confluent with a gap in the anterior part of the floor of the external naris in MCZ 2200. The condition of this region in MCZ 1371 and 1438 is not clear but appears to be similar in the former at least. A comparable situation exists in *Eupelor* (*Buettneria*).

The choanae are located halfway between the anterior end of the interpterygoid vacuities and the end of the snout. They are suboval in outline, with a length of approximately 1.5 cm and a greatest width of .6 cm. Anteriorly, they are constricted by a lateral curvature of the medial border. The lateral margin of the choana is formed in the main, and perhaps entirely, by the palatine, the anterior and medial margins by the vomer. Although the palate was crushed against the ventral surface of the skull roof in this region of the type specimen, it is apparent that the vomer formed a stout rim on the medial and anterior borders of the opening. The anterior ends of the choanae are 1 cm behind the level of the posterior rims of the external nares. Therefore, to reach the internal naris from the outside, air had to pass backward through a short passageway between the skull roof and the palate—a passageway surely enclosed in a cartilaginous nasal capsule.

The central palatal surface anterior to the interpterygoid vacuities is formed by the vomers. These bones, conforming to the contours of the snout, are approximately four times as long as they are wide. Anteriorly, the vomer is bounded by the premaxilla, and forms the posterior rim of the anterior palatal fenestra; laterally, it joins the maxilla and the palatine, and forms the medial and posterior boundaries of the choana. The vomer meets the palatine midway on the posterior rim of the choana. The suture between the two bones appears to run diagonally backward and outward, medial to the palatine tooth-row. Posteriorly, the vomer forms the anterior margin of the interpterygoid vacuity, but the two vomers are separated in the midline, posteriorly, by the wedge-shaped anterior end of the cultriform process of the parasphenoid. At the point where the vomers meet medially the end of the cultriform process appears to pass dorsal to them.

The posterolateral sutural relations of the vomers are obscured by numerous cracks and the poor preservation of the palatal surface. However, it appears that the vomer formed the anterolateral border of the interpterygoid vacuity, retaining a primitive contact with the pterygoid medially near the anterior end of that opening.

The palatine is bounded laterally by the maxilla and medially by the vomer. Posteriorly, the palatine meets the ectopterygoid. This suture was hard to find but appears to run diagonally forward across the palatal toothrow immediately in front of an enlarged tooth pair and 2.5 cm behind a pair of palatine tusks. If this is the correct position of the suture, the ectopterygoid bears a pair of tusks at its anterior end. It is of interest to note that in *Trimerorhachis*, as described by Case (1915), the ectopterygoid is a short bone, and the palatine supports not only an anterior fang pair but a second pair of enlarged teeth as well. No enlarged tusks occur on the ectopterygoid in that form. A review of the literature failed to uncover any different description of the palatine-ectopterygoid suture in *Trimerorhachis*. Thus, if the present interpretation is correct, *Neldasaurus* is more primitive than *Trimerorhachis* in this respect.

Assuming that the position of the suture is correct, the ectopterygoid is a long bone, about equal in length to the palatine. Medially, it is bounded by the palatal ramus of the pterygoid and laterally by the maxilla. Posteriorly, where it enters the anterior border of the subtemporal fossa, it is very narrow.

The palatine and ectopterygoid are thickened under the palatal tooth row, and join the maxilla in a firm articulation on the medial surface of that bone. The palatine is stouter than the ectopterygoid. The union of these lateral palatal bones with the maxilla does not reach the ventral edge of the latter with the result that, in ventral aspect, there is a shallow longitudinal groove along the lateral edge of the palate just inside the skull margin.

In primitive fashion, the vomer, the palatine and, apparently, the ectopterygoid each bears a pair of tusks. Those of the palatine are the largest and those of the ectopterygoid are the smallest. It was not possible to determine whether or not any small teeth were present on the vomers between the choanae. However, both the palatine and ectopterygoid tusks are accompanied by a single row of small teeth.

On the left side of the palate in the type specimen the vomerine tusk pair is represented by an empty socket with a tusk behind it. On the right the conditions are reversed. The vomerine tusk is .5 cm in diameter near the base and is somewhat over 1 cm long.

The right palatine bone also supports a tusk pair at its anterior end, the posterior tusk represented by an empty socket. The palatine tusk preserved is larger than that of the vomer, with a diameter at the base of .6 cm and an approximate length of 1.2 cm. Behind the tusk pair on the palatine is a close-set row of 8 small teeth. The more anterior ones are oval in outline, their long axes perpendicular to the tooth row. The posterior ones are round in section. Larger than the maxillary teeth, the palatine teeth average 2 mm in diameter. The third pair of tusks is located at the anterior end of the ectopterygoid. The anterior member of the pair has a basal diameter of 3 mm, and the posterior a diameter of 4 mm. Behind these, extending nearly to the end of the ectopterygoid, is a row of 21 teeth, decreasing slightly in size towards the posterior end of the row. Their diameter at the base is about 1 mm.

The pterygoid of the type specimen, though damaged, is nearly complete. There are also portions of pterygoid bones in MCZ 2406 and 2407.

The pterygoid consists of a horizontal palatal ramus, a stout central body and a vertical quadrate ramus. The curved, medial margin of the palatal ramus forms the lateral and posterolateral borders of the interpterygoid vacuity. The bone in general is fairly stout but is thin at its medial edge. The palatal ramus has a narrow anterior process, bounded laterally by the ectopterygoid, which articulates with the vomer anteriorly. The posterior portion of the palatal ramus is expanded horizontally. The outer edge of the pterygoid is here thickened and turned ventrally to form a flange about 1 mm deep which forms the anterior portion of the medial border of the subtemporal fossa; the remainder of the border is supplied by the central body and the quadrate ramus of the pterygoid.

The basal articulation was apparently movable (Fig. 4, A). The thickened, horizontal body of the pterygoid opposite the

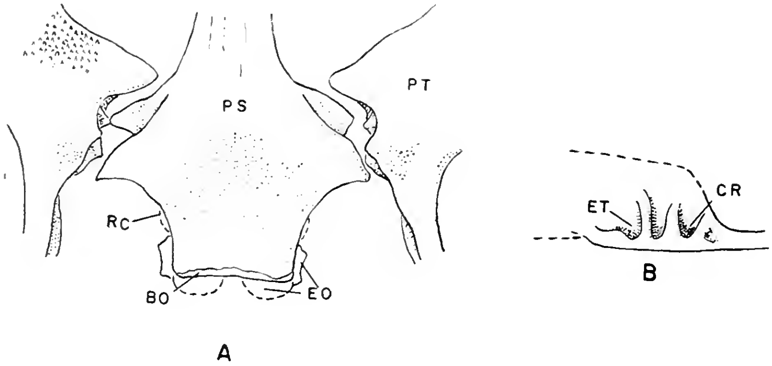

FIG. 4. *Neldasaurus wrightae.* A, reconstruction of the basal articular region of the skull of MCZ 2200 in ventral view, × .75. (Evidence for the presence of the teeth shown on the right pterygoid based on MCZ 2406 and 2407). B, projection of a portion of the medial surface of the left palatoquadrate of MCZ 2200, × .75. Abbreviations: BO, basioccipital; CR, conical recess; EO, exoccipital; ET, "excavatio tympanica"; PS, parasphenoid; PT, pterygoid; RC, pocket for rectus capitus muscle ?

basal articular region of the basisphenoid has an internal process that presumably articulated with the basipterygoid process of the braincase. The internal process, seen best on the right in MCZ 2200, curves dorsally from the level of the central body of the pterygoid so that its tip is nearly .5 cm above the lower surface of the bone. An ascending process rises from the medial edge of the pterygoid just behind the tip of the internal process. Its height above the internal process is about .5 cm, but it rises rapidly posterior to this point to a height of 1.7—1.8 cm opposite the basipterygoid process of the braincase. The concave posterior face of the internal process of the pterygoid forms the anterior and ventral walls of a socket or ''conical recess'' for the reception of the basipterygoid process of the braincase. The back wall of the ''conical recess'' is formed by an essentially vertical ridge that rises from the dorsal surface of the pterygoid, just inside the medial edge of the bone, about 1 cm behind the tip of the internal process. This leaves a very limited socket for the reception of the basipterygoid process. Behind the ridge there is a vertical groove, about 5 mm wide, which separates the ridge from the anterior end of the vertical quadrate ramus (Fig. 4, B). The latter, rising above a small medial projection of the pterygoid, forms a second ridge posterior to the groove. The posterior face of the ridge thus produced at the root of the quadrate ramus, and the medial face of the quadrate ramus adjacent to it, share a concavity just above the ventral surface of the pterygoid. It is obvious that this deeply excavated area represents the ''excavatio tympanica'' of Bystrow and Efremov (1940). It appears that *Neldasaurus* is unusual in that the posterior wall of the ''conical recess'' is separated by a groove from the ascending ridge at the base of the quadrate ramus which forms the anterior wall of the tympanic excavation.

The quadrate ramus of the pterygoid is approximately 4 cm long and curves outward slightly as it proceeds from its root to an attachment with the quadrate at the outer posterior corner of the skull. Just behind the root, the quadrate ramus, as noted, becomes more or less vertical in the skull, apparently ascending dorsally and somewhat medially. Near the level of, or just anterior to, the otic notch the vertical flange of the quadrate ramus overlaps on the medial side a vertically descending flange of the squamosal. The posteromedial face of the quadrate ramus appears to have had an irregular surface, marked by longitudinally oriented ridges and grooves. There is a prominent, more or less horizontal, elongate groove in the quadrate ramus, just below its connection with the descending flange of the squamosal. Although post-mortem flattening of this region has introduced some uncertainty in dorsoventral relationships, it seems highly probable that this groove is homologous with the groove in the posteromedial face of the quadrate ramus of *Trimerorhachis,* which apparently serves as a floor for the tympanic cavity (Watson, 1956).

Little can be seen of the quadrate bone. On the medial side of the left cheek in the holotype, however, an anterior extension of the quadrate, which diminishes in size anteriorly, meets the squamosal dorsally and the quadrate ramus of the pterygoid ventromedially.

There is no evidence of an ossified epipterygoid in *Neldasaurus.* A review of the *Trimerorhachis* materials in the collection of the Museum of Comparative Zoology confirmed earlier reports that there is no ossified epipterygoid in that form either.

The obstinate character of the matrix left no indication of palatal teeth in areas other than those described in MCZ 2200, but the fragments of the pterygoid bones in MCZ 2406 and 2407 show that the horizontal flange and part of the palatal ramus are covered by a densely-packed shagreen of small teeth except at the medial edge of the bone.

Parasphenoid and Braincase

The braincase is fairly complete in ventral aspect in the holotype specimen. The dorsal surface is crushed against the underside of the skull roof and little can be seen of the lateral surface. The only other braincase material consists of a badly weathered partial parasphenoid with MCZ 1438 and a small portion of the left side of an isolated parasphenoid in MCZ 2518. The description of the parasphenoid and the braincase is based on the holotype.

The proportions of the braincase are remarkably similar to those of *Trimerorhachis* (Case, 1935; Watson, 1956). The sphenethmoid region is narrow, but behind its articulation with the pterygoids the braincase is expanded and more or less flattened. As is usual, the ventral surface of the braincase is sheathed by the parasphenoid.

The parasphenoid narrows gradually in front of the basipterygoid process of the braincase, giving rise to an anteriorly directed cultriform process, which forms the medial border of each interpterygoid vacuity. The cultriform process is about 6.6 cm long, fairly broad at each end, but narrow in the central region. The anterior end of the process is wider than in *Trimerorhachis,* but it does not project as far forward into the anterior palatal surface as it does in such forms as *Saurerpeton* or the Triassic metoposaurs.

The anterior and posterior portions of the ventral surface of the cultriform process are nearly flat; the central portion is ventrally convex in cross section, the lateral edge being approximately 2 mm above the level of the ventral surface. The surface of the cultriform process is marked by fine longitudinal ridges and grooves, which also appear to some extent on the main body of the parasphenoid. There is no evidence of teeth on the ventral surface of the parasphenoid, though the rigorous preparation required to remove the matrix could have obscured them.

The main body of the parasphenoid is broad and essentially flat in ventral view (Fig. 4, A). Behind the root of the cultriform process the parasphenoid expands laterally, the central region between the laterally expanded ''wings'' being moderately concave. Laterally, the parasphenoid sheaths the anterior, ventral and posterolateral faces of the basipterygoid process. The ''core'' of the process, ossified as part of the basisphenoid in many labyrinthodonts, was here apparently cartilaginous. It would have been exposed at the tip of the process above the parasphenoid, where it could have entered the ''conical recess'' of the pterygoid to meet the cartilaginous epipterygoid. The anterior margin of the parasphenoid covering the basipterygoid process is directed diagonally outward and backward in direct apposition to the posterior margin of the internal process of the pterygoid. As in *Trimerorhachis,* but in no other Permian temnospondyl, the articular process of the parasphenoid is set off from the main body of the bone by a groove which runs diagonally outward and backward, widening and increasing in depth distally. The anteroventral rim of the articular process of the parasphenoid issues from the side of the braincase on the same level as the ventral surface of the main body of the bone.

Behind the basipterygoid processes, the parasphenoid expands laterally to a width of approximately 5 cm. The margin of the bone then curves sharply inward, matching posteriorly the width of the basioccipital which is 2.2 cm across the base. The posterior border of the braincase has been damaged, but it appears that the parasphenoid reaches, or nearly reaches, the posterior ventral rim of the basioccipital, although it is extremely thin at this point.

A lateral extension of the parasphenoid turns upward on either side around the basioccipital, gaining a narrow exposure on the lateral face of the braincase at the level of the condyle. Anteriorly this lateral exposure increases, attaining a height of nearly 5 mm ventral to the fenestra ovalis, the ventral rim of which was apparently formed by the parasphenoid. The dorsal and lateral margins are incomplete. In *Trimerorhachis* the lateral concave face of the parasphenoid behind the basipterygoid process contains a deep pocket ventral to the fenestra ovalis, which Watson suggests could have received a rectus capitus muscle. Although this region in *Neldasaurus* is not complete, the details that can be seen suggest that a similar, though less pronounced, fossa for muscle insertion was present.

Careful scrutiny failed to disclose the presence of any openings for the palatine or internal carotid arteries in the ventral or lateral surfaces of the parasphenoid. However, these openings are often small and are not consistently demonstrable even in a well known form like *Trimerorhachis*. Failure to find them in *Neldasaurus* can probably be attributed to their small size or to the rigorous treatment necessarily employed in removing the matrix from the surface of the bone.

Some features of the dorsal surface of the parasphenoid can be determined from exposed portions of the lateral edges, and from the face of a break which runs diagonally across the main body of the braincase. The outer end of a broad groove in the dorsal surface of the parasphenoid can be seen on the lateral surface of the braincase above the laterally expanded "wing." The groove is 6 mm wide at its lateral end and is directed anteromedially. It appears to be comparable to a similar groove on the upper surface of the parasphenoid in *Trimerorhachis* and, as Watson (1956) suggests, probably sheathed the lower medial end of the prootic.

Immediately anterior to the basipterygoid process, the lateral edge of the parasphenoid is thin, but both faces of a break in this region exhibit a thickened mass of bone. Although the form of this thickened mass is partially obscured by matrix, it appears to be part of a strongly developed transverse ridge of bone on the upper surface of the parasphenoid between the roots of the basipterygoid processes. The ridge could occupy the position to be expected of the posterior rim of a depression for the pituitary.

Reduction of ossification in the braincase is well advanced. The basisphenoid and otic capsule were apparently cartilaginous, since neither is preserved in the holotype. There is, however, evidence of an ossified sphenethmoid. A flat bone about 1 cm high appears to occupy the space between the cultriform process and the skull roof from the anterior end of the interpterygoid vacuity back to a point not far in front of the level of the parietal foramen, a distance of about 4 cm. This bony sheet, bounding laterally the space above the cultriform process, undoubtedly represents an ossified sphenethmoid of the right side. There is no evidence that there was any lateral expansion of the bone like that seen in *Edops* and *Eryops*. Unfortunately, the stapes is not preserved in any specimen.

OCCIPUT

(Figure 5)

The occipital region of the holotype, though damaged, is nearly complete and can be restored. An isolated partial condyle among the materials associated with MCZ 1371 also offers some information, but the description is based mainly on the holotype. The occipital region of MCZ 2200 has been subjected to postmortem flattening, resulting in some dislocation of its parts. The dorsal portions of the exoccipitals are missing, and only the left side of the condyle is reasonably intact.

The incomplete nature of the exoccipitals hindered an attempt to get an accurate picture of the proportions of the occiput.

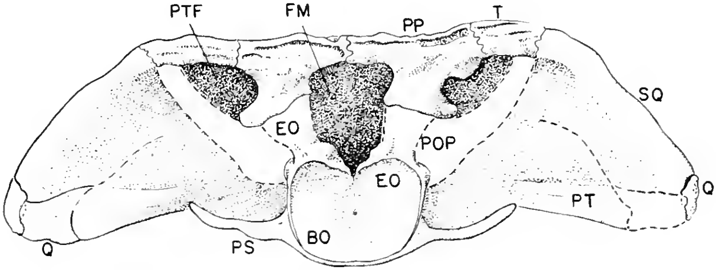

FIG. 5. *Neldasaurus wrightae* (MCZ 2200 and MCZ 1371). Reconstruction of the skull in occipital aspect, × .75 approx. Abbreviations: BO, basioccipital; FM, foramen magnum; POP, paraoccipital process; PS, parasphenoid; PT, pterygoid; PTF, posttemporal fossa. Other abbreviations as in Figure 1. Restored features are in dotted lines.

However, on the basis of the general similarity of the structure and proportions of the occipital region of *Neldasaurus* and *Trimerorhachis,* the height of the dorsal portions of the exoccipitals of *Neldasaurus* was estimated by comparison with Watson's figures for *Trimerorhachis.* Accordingly, the height of the occiput of *Neldasaurus* was approximately 3.9 cm. As noted earlier, the backward slope of the occiput was probably not pronounced in life.

The occipital condyle is a single, subcircular structure with a concave posterior face. Its lower division is formed by the basioccipital, best seen in MCZ 1371. The basioccipital is wedge-shaped in lateral view and extends forward ventrally into the floor of the braincase for a distance of approximately 1.5 cm. The dorsal surface of this anterior extension is unfinished. As said earlier, the parasphenoid covers the ventral surface of the basioccipital to, or nearly to, its posterior border. As in *Trimerorhachis,* the ventral surface of the basioccipital has longitudinal ridges which were in contact with the upper surface of the parasphenoid.

The exoccipitals, resting directly on the basioccipital, form the dorsolateral portions of the condyle and complete its concave posterior face. The position of the suture between the basioccipital and exoccipital can not be determined with certainty but appears to be about half-way between the base and the top of the condyle. Dorsally, the condylar portions of the exoccipitals are well separated, but they approach each other in the midline ventrally. Above the center of the condyle, which contains a notochordal pit, the exoccipitals are only separated by a narrow groove. Above the condyle the exoccipital had a dorsal process, represented in the specimens by its basal portion only, which formed the lateral wall of the foramen magnum and articulated dorsally with the inferior surface of the descending flange of the postparietal. Anteriorly, a projection of the basal portion of the exoccipital of each side extends forward in the floor of the braincase above the anterior extension of the basioccipital, but details are obscure. Probably, as in *Trimerorhachis,* it provided a floor for the medullary region of the braincase. These anterior extensions of the exoccipitals do not quite meet in the midline. The structure of this region, in so far as it can be determined, corresponds generally to that described for *Trimerorhachis* by Watson.

Anterior and somewhat lateral to the base of the dorsal extension of the exoccipital, there is a small process of the exoccipital which forms the anterior wall of the vagal foramen. The posterior wall of the foramen is formed by the base of the ascending process of the bone. Just posterior to the vagal foramen the lateral wall of the exoccipital is pierced by a singe foramen for nerve XII. The inner opening of this foramen is in the medial surface of the bone, anterior and slightly ventral to its lateral exit, as seen in MCZ 1371.

The ventral surface of the condyle is broad and more or less flat. The width of the condyle in MCZ 2200 is 2.2. cm and its height is 1.7 cm, while the isolated condyle of MCZ 1371, with a width of 2.3 cm and a height of 1.3 cm, is even lower. These proportions seem to reflect a general trend towards flattening in *Neldasaurus.* The lateral sides of the condyle rise abruptly from the more or less flattened base. In lateral aspect they are considerably narrower than the sides of the condyle in *Trimerorhachis.* Taken together, these characteristics of the condyle resemble the proportions of the intercentra of *Neldasaurus,* in which slender, upright lateral processes arise from the edges of a broad ventral base.

The occipital exposure of the postparietal has a slight backward slope, which is interpreted as being normal. There is no supraoccipital ossification. The ventral articular surface of the postparietal flange slants laterally and ventrally at an angle of 45 degrees to the horizontal, ending laterally in a blunt point. The medial portion of this flange presumably articulated with the upper end of the exoccipital; the laterally projecting outer corner may have rested on the base of a cartilaginous paroccipital bar. There is some evidence that a cartilaginous paroccipital bar extended between the exoccipital and the tabular. The upper end of the bar could have been received in the fossa in the ventral surface of the tabular already described. The lower end of the bar presumably met the anterior surface of the exoccipital ventromedially. There is no indication that the tabular or the exoccipital invaded the paroccipital bar, the latter thus forming the whole of the lower boundary of the posttemporal fossa. The remainder of the fossa, as in *Trimerorhachis,* is formed by the postparietal and the tabular.

Lower Jaw

(Figure 6)

All of the lower jaw specimens have suffered some post-mortem damage and distortion, especially in the articular region. The most complete jaws, MCZ 2200, 1371 and the anterior portions of 1438, are crushed against the ventral surface of the skull so that much of their dorsal and medial surfaces is obscured. Fragments of lower jaws are also present in MCZ 2516, 1381, 1463, 2406, 2404, and 2518.

The right jaw of the holotype specimen is well preserved throughout its prearticular extent, the articular region being hidden. The left jaw is nearly complete from front to back in ventral aspect, the articular region, though twisted, retaining its connection with the prearticular ramus. The infradentary portions of both jaws have been flattened against the palate, losing their original relation to the vertical plane of the dentary.

The left lower jaw of MCZ 1371 (Fig. 6, A) has undergone some distortion and damage, but the preservation of the surface permits a more accurate tracing of the suture pattern than either jaw in MCZ 2200. The anterior tip is missing, but the contours of the preserved portion permit an accurate restoration. Also, though it is incomplete, the articular region is more readily visible in this specimen.

The reconstruction of the lower jaw shown in Figure 6, B is a composite, based primarily on MCZ 2200 and 1371. The relation of the articular region to the ventral rim of the jaw is based on this portion of a small jaw in MCZ 1381, but this relationship is, admittedly, subject to some uncertainty in the larger specimens where the articular region has shared in the general flattening of the ramus.

Aside from a few details, the lower jaw of *Neldasaurus* closely resembles the lower jaw of *Trimerorhachis*. Viewed from below, the anterior end of the jaw is bluntly rounded, the end of each ramus swinging abruptly towards the symphysis from its lateral border, thus paralleling the blunt contours of the snout. The jaw is very shallow anteriorly, its strongly curved outer surface directed as much ventrally as it is laterally. Posteriorly, it becomes progressively deeper, and the convexity of the lateral surface, though continued, is less pronounced. The ventral rim of the jaw was apparently medial to the plane of the dorsal rim in life. The medial surface, forming a sharp angle with the lateral surface ventrally, is essentially vertical. Posteriorly, the ventral margin of the jaw curves sharply upward to the articular region. There is a modest retroarticular process which extends for a distance of 6 mm behind the posterior rim of the glenoid fossa on the medial side of the jaw. Two cm behind the anterior end of the jaw the dorsal edge of the dentary rises to a point 3 mm above its anterior level; 3 cm behind this point a second, though less abrupt, increase in height occurs. From here, the dorsal margin of the jaw rises gradually to the articular region.

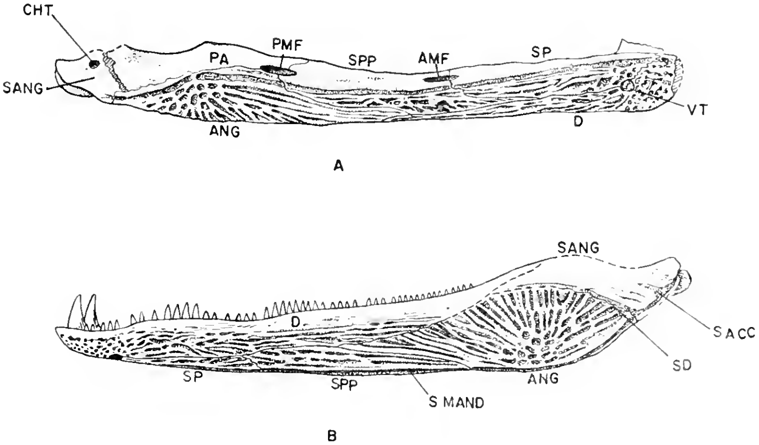

Fig. 6. Lower jaw of *Neldasaurus wrightae* × .50. A, ventral view of left ramus of MCZ 1371. B, external view of left ramus restored (based mostly on MCZ 2200 and MCZ 1371). Abbreviations: AMF, anterior Meckelian fenestra; ANG, angular; CHT, foramen for chorda tympani; D, dentary; PA, prearticular; PMF, posterior Meckelian fenestra; SACC, accessory sulcus; SANG, surangular; SD, dentary sulcus; SMAND, mandibular sulcus; SP, splenial; SPP, posterior splenial; VT, fenestra for reception of vomerine tusk.

The bones of the outer surface of the jaw are sculptured. The medial surface and the ventral rim are smooth.

Two narrow, elongate Meckelian fossae are present just above the ventral margin on the inner surface of the jaw. There is a foramen for the chorda tympani just under the edge of the glenoid fossa at the root of the retroarticular process on the medial surface of the jaw.

In the discussion of the palatal dentition, a fenestra for the reception of a vomerine tusk in the lower jaw was mentioned. In both lower jaws of MCZ 2200 and 1438 and the single jaw of 1371 there is a hole that penetrates the jaw from top to bottom to accommodate the tip of a vomerine tusk. That this is not the result of post-mortem flattening of the skull is shown by the absence of breakage of the surface bones and the finished rim of the opening. The opening of the fenestra in the ventral surface of the jaw is suboval in outline, the long dimension being directed anteromedially. It is approximately 4 mm wide and 5 mm long, and is located on the suture between the dentary and the splenial at, or slightly behind, the level of the posterior limit of the symphysis. In MCZ 2200 a second fenestra is present in the anterior end of the postsplenial for the accommodation of a palatine tusk. This second fenestra, however, is not evident in MCZ 1371 or 1438.

Colosteus scutellatus and *Erpetosaurus radiatus* (Romer, 1930) have a groove in the outer surface of the lower jaw for the reception of a large premaxillary fang. Some Crocodylidae have developed fossae which penetrate the upper surface of the anterior end of the snout for the lower jaw fangs and, of course, anterior palatal openings are present in a large number of temnospondylous labyrinthodonts. But perforation of the lower jaw for the accommodation of an upper jaw tusk appears to be unique in *Neldasaurus*.

The absence of the posterior fenestra in two of the skulls may reflect individual variation in the depth of the jaw in relation to the length of the tusks, or perhaps in older animals large tusks may gradually wear a smooth opening through the lower jaw.

The symphysis is formed by the dentary anteriorly, and the splenial (presplenial) forms the posterior half. Ventrally, it is approximately 1.5 cm long; dorsally it is 2.2 cm long. A medial expansion of the splenial near its anterior end meets a similar expansion from the opposite side, thus lengthening the extent of the symphysis dorsally. The posterior border of the medial process so formed lies 1 cm above the ventral rim of the jaw. A somewhat similar condition appears to obtain in *Trimerorhachis*, though developed to a lesser degree.

The dentary occupies most of the upper portion of the lateral surface of the jaw ramus and, as already shown, forms most of the anterior end of the jaw. Except for some uncertainty concerning the posterior extent of the dentary, its relation to the other dermal elements is similar to that of other rhachitomes. It is bounded ventrally by the splenial, postsplenial and angular from front to back, and overlaps each of these elements to a variable extent. The dentary narrows abruptly at the back, its ventral edge ascending diagonally upward and backward. Although its relation to the surangular is not clear, an anterior process of the surangular appears to be interjected between the upturned posterior end of the dentary and the dorsal border of the angular. Much of the dentary is sculptured, but the dorsal portion along the tooth row is quite smooth except for the presence of fine, longitudinal striations.

The splenial, as stated, forms the posterior portion of the symphysis, its anterior end meeting the dentary in a serrate suture. On the outer surface of the jaw it has a long diagonal external suture with the postsplenial, which slants downward and backward, and internally reaches the anterior Meckelian fenestra, forming the anterior rim of that opening.

The postsplenial extends posteriorly to the posterior Meckelian fenestra, forming the anterior third of the border of that opening. Posteriorly, it has a ventrally directed, diagonal suture with the angular on the lateral surface of the jaw. The postsplenial turns over the ventral rim of the jaw, appearing at the level of the posterior Meckelian fenestra to have a height well over 1 cm on the medial surface.

The large angular forms the posteroventral rim and most of the lateral surface of the jaw below and anterior to the articulation. Posteriorly and dorsally the angular is bounded by the surangular, anteriorly and dorsally by the dentary. It has a rather long anterior extension, confined to the lateral face of the ramus, which projects between the postsplenial and the dentary in a gradually narrowed process. Ventrally, a suture between the angular and the prearticular is located on, or just medial to, the ventral rim of the jaw.

The surangular is not complete in any of the specimens. However, on the medial surface of the articular region of the jaw of MCZ 1371 a rather large crack slants upward and backward from the end of the angular to the lip of the glenoid fossa. In the absence of other evidence, and because of its position, this ''crack'' is tentatively identified as the suture between the surangular and the prearticular. Thus, the surangular would form the posterior border of the glenoid fossa. Immediately posterior to the "suture," and, as noted previously, just under the edge of the glenoid fossa, is a foramen for the chorda tympani. Its dorsal position and the fact that it is nearly, if not completely, surrounded by the surangular contrasts to the situation in *Trimerorhachis*. In that form, the surangular, angular and prearticular all contribute to the borders of the foramen, according to Case's figures, and its position is more ventral. The foramen for the chorda tympani in MCZ 2200 has a lower position than that observed in MCZ 1371, suggesting that its location is subject to individual variation.

The limits of the articular bone can not be determined and a dorsal view of the glenoid fossa is seen only in MCZ 1371. Unfortunately, it has been damaged. The fossa consists of a concave depression passing diagonally inward from the outer posterior corner of the jaw. A slight ridge separates an outer articular facet from a longer facet on the inner side of the fossa.

The full extent of the prearticular can not be determined, nor can its relation with the coronoids be seen in surface view. In typical fashion it forms the medial wall of the adductor fossa above the angular and postsplenial. Its anterior end extends for some distance in front of the posterior Meckelian fenestra. The medial edge of the adductor fossa is, as typically, lower than the lateral edge. The fossa appears to end anteriorly at the level of the posterior rim of the posterior Meckelian fenestra, having a length of approximately 4 cm.

Unfortunately, the coronoid series is not visible in any of the specimens. The only source of information is that supplied by cross sections of the right lower jaw of MCZ 2200 (Fig. 7). A section through the anterior coronoid, Section J_1, shows three small teeth in a transverse series. Presumably these teeth represent the condition continued throughout the rest of the bone. Traces of similar small teeth were also found in sections showing the other coronoid elements in *Neldasaurus*.

Section J_1 was made approximately 3.5 cm behind the tip of the jaw and 2.3 cm in front of the anterior end of the anterior Meckelian foramen. It should, therefore, pass through the dentary, the splenial and the anterior coronoid. As can be seen in the figure, some distortion is evident, but the three elements can be identified.

A comparison of this section with a section taken through the anterior end of the jaw of *Trimerorhachis* (Broom, 1913, fig.

9D) demonstrates a basic similarity in structure, though the jaw of *Neldasaurus* is relatively more narrow.

Section J_2 was made approximately 1 cm in front of the posterior Meckelian foramen. This section shows very clearly a medial extension of the dentary below the tooth row and above the Meckelian space. The lower portion of the jaw has been folded medially to the vertical plane of the dentary. If this were drawn back to a reasonably normal position, the height of the jaw at this level would be approximately 1.8 cm and the ventral rim would lie a considerable distance medial to the lateral surface of the upper border of the dentary.

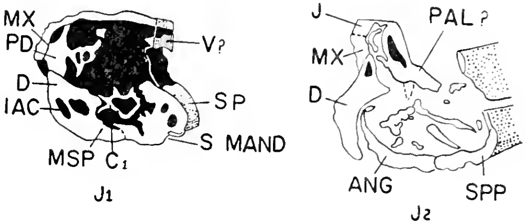

FIG. 7. Transverse sections of the right lower jaw and lateral palatal border of MCZ 2200, × 1. J_1, Section 3.5 cm behind the anterior end of the ramus; J_2, Section 1 cm in front of the posterior Meckelian foramen. Abbreviations: C_1, anterior coronoid; IAC, inferior alveolar canal; MSP, Meckelian space; PD, palatal debris; V?, vomer. Other abbreviations as in previous figures.

The sensory canal system of the lower jaw appears to be represented by three lateral line grooves — a mandibular, a dentary, and an accessory. The mandibular sulcus originates on the posterior margin of the jaw, lateral to the retroarticular process. Its course is readily traced in MCZ 1371 and 2200, where it proceeds along the ventrolateral edge of the jaw, just above the ventral rim, to the posterior border of the symphysis.

The dentary sensory groove arises from the mandibular groove below the articular region, and runs forward along the upper margin of the angular. Anterior to the midpoint of the angular it can not be traced with certainty.

There is some evidence in MCZ 1463 and in the small jaw of 1381 of the presence of an accessory sulcus, dorsal to the dentary sulcus, at the posterior end of the jaw. Due to poor preservation it can not be positively identified in either 1371 or 2200.

By piecing together the information that can be obtained from MCZ 2200 and 1371, it is possible to give a fairly complete account of the lower jaw dentition. *Neldasaurus* possesses a pair of prominent symphysial tusks on either ramus, each with a diameter at the base of about 5 mm and a height of at least 1 cm.

The teeth of the dentary series in MCZ 2200 and 1371 agree generally in size and number in comparable sections of the jaws of the two specimens, and it appears that the lower jaw of *Neldasaurus* contained 60 or so teeth. The teeth are more crowded than they are in *Trimerorhachis* (where there are about 48 teeth in the lower jaw), a feature which reflects the high tooth count of the maxillary series already described.

An attempt to recognize a consistent pattern of tooth replacement was unsuccessful.

There is a gradual reduction in tooth size from front to back, but with some suggestion of regional enlargement not far behind the anterior end of the dentary in MCZ 2200. The teeth in MCZ 1371, though all have lost their tips, are better preserved than in either jaw of MCZ 2200. Again, there is regional enlargement of the teeth somewhat behind the anterior end of the tooth row. Near the anterior end of the dentary the teeth have a diameter at the base of 1.75 mm. The enlarged teeth that follow have a diameter of 2.5-3.0 mm. In the lower jaw tooth series here described, teeth 18-22 are enlarged, 21 and 22 being the largest. Comparison of the position of this series with the palatal dentition shows that these teeth would be located between the vomerine and palatine tusks, though closer to the latter. Behind this series a second, though less pronounced, enlargement occurs in teeth 33-38.

VERTEBRAL COLUMN

(Figures 8 and 9)

In addition to numerous isolated elements, mostly centra and intercentra, three specimens show associated vertebral material in more or less continuous series.

The vertebral column of MCZ 2200 is distorted and much of the detail is obscure. However, it is possible to trace a reasonably continuous presacral column in which there were approximately 34 vertebrae. MCZ 2518 includes a number of blocks containing presacral vertebrae and several isolated elements, including 33 intercentra. Twenty-five vertebrae can be accounted for in MCZ 1371. It seems probable, therefore, considering the possibility of loss of some elements, that *Neldasaurus* had approximately 34 presacral vertebrae. The estimated number for *Trimerorhachis* is 31 (Williston, 1915; Case, 1935).

Unfortunately, no atlas vertebra was found and there are only three elements possibly belonging to the caudal series.

On the basis of the relative positions of the vertebral elements in blocks, variations in size of the elements, and variations in the height of the rib facets on centra and intercentra, the presacral vertebral columns of MCZ 2200, 1371 and 2518 were reconstructed.[1] The similarity of the vertebrae of all the *Neldasaurus* specimens makes a detailed description of each specimen unnecessary.

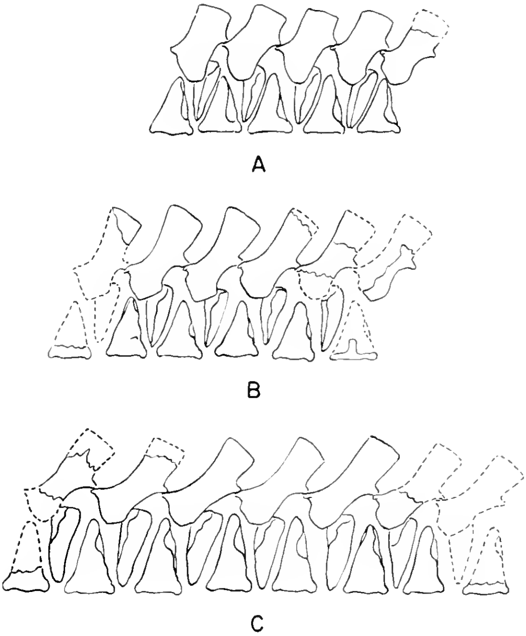

FIG. 8. Partial reconstruction of presacral vertebral column of *Neldasaurus wrightae*, × .5. A, vertebrae 2-5; B, vertebrae 11-16; C, vertebrae 19-26.

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[1] A detailed description of the reconstruction of the vertebral column for each specimen is given in the thesis on which this paper is based, on file at Harvard University.

The *Neldasaurus* vertebrae conform closely to the typical rhachitomous pattern. Each vertebra consists of a neurocentrum, a single intercentrum open at the top, and paired lateral pleurocentra. The latter are well developed and have a height approximately equal to that of the intercentra. Figure 9, A and B, shows three vertebrae from the mid-dorsal region and two vertebrae from the anterior dorsal region of MCZ 1371.

There is little regional difference in the size of the intercentra and pleurocentra of the presacral vertebral column. Those of the mid-dorsal region are slightly larger than the elements of the anterior and posterior regions. The average height of the first ten intercentra in MCZ 1371 is 1.9 cm, and the average length of the base is 1.2 cm. In the mid-dorsal region these figures are 2.2 cm and 1.5 cm, respectively. Elements near the posterior end of the series are intermediate in size between the anterior and mid-dorsal elements.

The intercentrum has an expanded, somewhat thickened base, from the lateral edges of which tapering, dorsally-directed processes curve upward around the notochordal space, giving a tall wedge-shaped appearance in side view. The ascending process ends in a blunt point. In none of the specimens do the intercentra form complete rings, though the dorsal tips of some approach each other quite closely. The ascending process is marked off from the base, on the lateral face of the intercentrum, by a usually prominent longitudinal ridge. Above the ridge the lateral face of the ascending process is concave. In ventral aspect the base of the intercentrum is widest posteriorly. Both anterior and posterior edges of the base are protuberant, having a medial swelling which is usually more developed anteriorly. The anterior and posterior edges of the base turn down so that the central region is modestly concave in lateral view. However, this concavity is not uniform, and in most intercentra a low, median, rounded ridge interrupts the depression.

There is an articular facet for the capitulum of the rib on the posterior border of the ascending process. In some instances this is a strong laterally directed projection, in others it is less pronounced. The height of the facet above the base of the intercentrum becomes progressively greater from front to back in the vertebral column. In some anterior intercentra the facet is at the very base of the lateral face, while in the posterior ones it is at the tip of the ascending process. The intercentra are stouter and better ossified than those of *Trimerorhachis,* so that the notochordal canal is relatively smaller than in that animal.

However, the base of the intercentrum is not as highly ossified as it is in *Eryops*. The ventral face and the ascending process are sheathed by dense periosteal bone, but on the lateral face of the latter the finished bone does not quite reach the edge or the tip of the process. The ventral and lateral faces of some intercentra are marked to varying degrees by small pits, while others have a smooth surface. The occurrence and development of pits is highly variable in intercentra of comparable size, even from the same individual. Prominent longitudinal ridges are not a common feature of the outer surface of the base and ascending process of the intercentra of *Neldasaurus* as they are in *Trimerorhachis*.

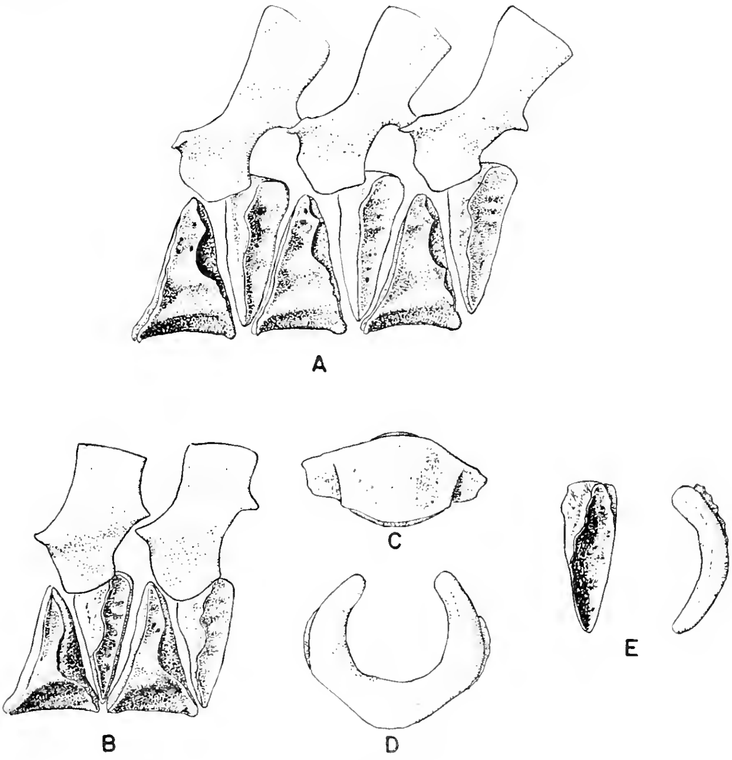

FIG. 9. Vertebral elements of *Neldasaurus wrightae*, MCZ 1371. A, mid-dorsal vertebrae, left lateral aspect. B, anterior dorsal vertebrae, left lateral aspect. C and D, ventral and anterior view of an intercentrum. E, lateral and anterior view of a left pleurocentrum. All × 1.

Three partial intercentra, possibly referable to the caudal series, are present among the specimens. Two are associated with MCZ 2200; the other is an isolated element associated with MCZ 2518. The base is not flattened but strongly curved. Dense perichondral bone is confined to the ventral surface and one edge of the ascending process, the top of which is missing. The intercentrum base is thickened dorsally by endochondral bone which constricts the notochordal space. There is no evidence of haemal arches. In the absence of other information these elements are presumably intercentra of proximal caudals.

The pleurocentra, like the intercentra, are very uniform in structure. They are prominent elements, and, as noted, have a height approximately equal to that of the intercentra. They have a blunt, oblong, dorsal head, about twice as long as it is wide. The ventral end is pointed. Their shape is essentially that of a slender wedge with the tip down, and they are unusual in reaching nearly to the bottom of the intercentra. In these features they are in sharp contrast to the small diamond-shaped pleurocentra of *Trimerorhachis* or the blocky wedges of *Eryops*. The lateral face of the pleurocentrum is covered by a layer of dense bone that curves outward along the edges so that the surface is concave. There are modest transverse ridges within the vertical groove so formed, and small pits which, like those of the intercentra, are variable as to number and arrangement. The finished bone does not reach the anterior or dorsal border of the pleurocentrum. In some, the anterior, lateral edge of the bone is reflected to produce a small facet, which presumably shared with the intercentrum in supporting the capitulum of the rib. In anterior aspect the pleurocentra are strongly curved to fit the notochordal canal.

The neural arches are low and the presence of a narrow strip of unfinished bone surface between the lateral halves of the arch suggests that the arches were formed as separate lateral ossifications. There are well developed anterior and posterior zygapophyses, but there is no discrete transverse process. The pedicle of the arch is modestly developed and is more truncate than it is in such a form as *Eryops*. The tuberculum of the rib presumably articulated with the ventrolateral area of the base of the arch pedicle.

The articular faces of the zygapophyses are roughened, and that of the anterior zygapophysis slopes inward for the reception of the posteriorly and ventrally directed face of the posterior zygapophysis of the preceding arch. The neural spines are low and only moderately expanded from front to back.

The neural arch elements show greater regional variation than the central elements. Thus, the neural arches of the "cervical" region (Fig. 9, B) have low neural spines, the fourth neural arch from the front as preserved in MCZ 1371 being 2 cm high, the arch pedicle accounting for 50 per cent of the total height. The pedicle descends for a short distance below the zygapophysis, and is curved sharply outward in a strong lateral projection — an incompletely ossified transverse process. The neural spines of this region have a slight backward tilt. The neural elements of the mid-dorsal region are taller, the additional height resulting from elongation of the neural spine (Fig. 9, A). The height of neural element 12 is 2.4 cm; the height of the arch above the pedicle is 1.8 cm, 75 per cent of the total height. The pedicle is truncated and the anterior zygapophyses are only slightly above its base. The neural arch of this region does not have a laterally directed pedicle as does that of the anterior region. The posterior zygapophyses are well separated from the anterior processes on each arch as a result of the strong backward slant of the mid-dorsal spines, which have a sharper backward tilt than those of the anterior region.

Ribs

(Figure 10)

There are many ribs preserved in the specimens but most are fragmentary and only a few, confined to MCZ 1371, have retained their original association with the vertebrae.

With one possible exception, the ribs preserved appear to belong to the dorsal series. A fragment from MCZ 2200 seems to be the distal portion of a rib with a "finished" end, which may belong to the "cervical" region. The proximal end is missing. The portion of the shaft preserved is 2.2 cm long, slightly curved and oval in cross section. The shaft is uniformly slender, with a diameter of only 0.2 cm, in contrast to the heavier dorsal ribs described below.

There is some regional variation in the dorsal ribs and also variation between specimens, but a common pattern can be traced. The shafts of the dorsal ribs are only slightly curved, so that the distal ends of the ribs of opposite sides are well separated ventrally. A rough calculation of the distance spanned by

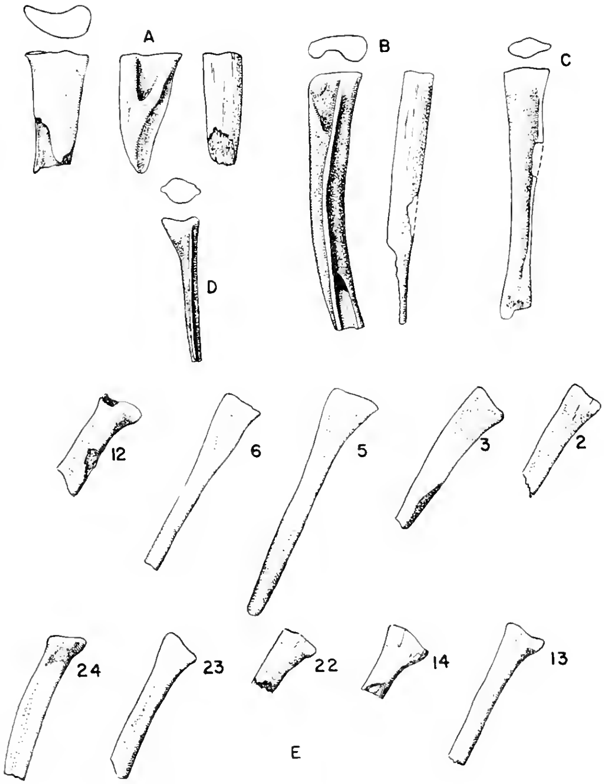

FIG. 10. Ribs of *Neldasaurus wrightae*. A and B, partial anterior ribs. C, partial rib from the mid-dorsal region. D, partial rib from the posterior presacral region. Other ribs as numbered. All from MCZ 1371. All × .75, approx.

opposing ribs articulating with the vertebral column gives a figure of 11.5 cm. If articulated, the ribs would appear to run essentially straight out, suggesting a flat back (and belly) in *Neldasaurus*. As the longest ribs preserved are incomplete distally, and since no provision was made for a possible cartilaginous cap on the rib head, this figure is reasonable when compared to the width of the pectoral girdle, which is 13.6 cm. Though most of the ribs taper distally, a few appear to have had a modest expansion of the distal portion of the shaft. Proximally the shafts are more or less triangular in section; distally they are elliptical, the long axis of the ellipse oriented dorsoventrally. The rib heads are expanded, though single, and some distinction can be made between confluent capitular and tubercular articular areas.

As noted, there is variation between specimens, so the rib series of MCZ 2200 and MCZ 1371 are described separately. The ten largest ribs preserved in MCZ 2200 probably belong to the anterior region of the dorsal series, and are all of comparable size. Of these ribs, the longest as preserved is 4.5 cm and is representative (Fig. 10, B). The head, which was presumably continued in cartilage, is broad, measuring 1.0 cm in the long axis. Proximally the shaft is stout, having a width of .6 cm on the "capitular" (medial) side and tapering distally to a diameter of .4 cm at the end as preserved. There is no clear division of capitulum and tuberculum on the anterior face of the rib head but the posterior face contains a shallow V-shaped depression in the central proximal region separating a rounded capitular area from a narrow tubercular area. The lateral edge of the shaft bears a low, narrow keel. Behind the keel, along the posterodorsal surface of the rib, a groove runs the length of the shaft.

There are parts of 12 slightly smaller ribs, mostly fragments of the shaft region, presumed to belong to the mid-dorsal series. The longest and most complete of these is shown in Figure 10, C. The rib is incomplete distally but is 4.2 cm long. It is less massive than the anterior ribs; the shaft is more slender and the groove along the posterodorsal border of the shaft is less pronounced. Unlike the anterior ribs, the shaft is straight. There is almost no distinction between capitular and tubercular areas, though the head is flattened.

Posterior dorsal ribs are represented by a single incomplete rib and fragments of two others. The former consists of the head and 2.5 cm of the proximal portion of the shaft (Fig. 10, D). The shaft is slender, the lateral margin forming a thin keel. It does not appear to be grooved. The medial surface is not visible. The head, which is .7 cm long, is thickened and is expanded medially in the central proximal region, so that it forms a nearly oval articular area in end view, and is more sharply marked off from the shaft than the heads of the anterior ribs. There is no separation of capitular and tubercular regions.

The ribs of MCZ 1371 (Fig. 10, E) are similar to those of MCZ 2200, but none are as massive as the anterior dorsal ribs of the latter. Regional differentiation is less marked in this specimen. The longest rib as preserved, associated with the 5th vertebra of the anterior portion of the vertebral column, is 4.4 cm long. The shaft tapers distally and is slightly curved. The head is flattened, being .8 cm wide, but there is little differentiation between capitular and tubercular areas. The depression noted in the rib heads of MCZ 2200 is lacking. There is a keel along the lateral edge in the proximal half of the rib shaft.

The ribs associated with the mid-dorsal vertebrae in this specimen differ from the anterior ribs in that the heads, though broad, are less flattened. There is some indication of a longitudinal groove like that seen in the ribs of the holotype specimen. The ribs associated with the more posterior series of vertebrae here resemble the mid-dorsal ribs. They are all incomplete distally, the longest being 3.0 cm long.

Thus, the ribs of *Neldasaurus* show some decrease in size from front to back. The heads of the anterior and mid-dorsal ribs are more or less flattened, and the posterior ribs have an expanded head, oval in end view. In some (MCZ 2200), distinction between capitular and tubercular areas is strongly pronounced in the anterior ribs, modest or lacking in the mid-dorsal ribs. A lateral keel appears to be a common feature of the rib shaft. The rib shafts show little curvature.

APPENDICULAR SKELETON

Shoulder Girdle. Parts of the dermal pectoral girdle can be seen in three specimens. MCZ 2200 shows the ventral surface of the clavicles and part of the interclavicle on the underside of the block behind the skull (Plate 2). The anterior end of the right clavicle was broken off but remained in the matrix. The clavicles are pushed together along the mid-line, so that there is little ventral exposure of the interclavicle. Part of the lateral edge of the left clavicle can be seen in dorsal view on the upper side of the block. MCZ 1371 includes the posterior half of a clavicle and a small portion of the interclavicle. MCZ 2518 includes a number of sculptured fragments of the clavicular girdle.

The dermal pectoral girdle of *Neldasaurus* has been restored in ventral aspect in Figure 11. The clavicles are based mainly on MCZ 2200. The posterior portion of the interclavicle is drawn from MCZ 1371. Although the latter animal was somewhat larger than the holotype, the structure and proportions of the girdle are apparently identical.

The ventral dermal girdle of *Neldasaurus* forms a broad thoracic shield whose anterior end appears to have extended forward under the braincase to the level of the posterior end of the basipterygoid process of the paraspheniod.

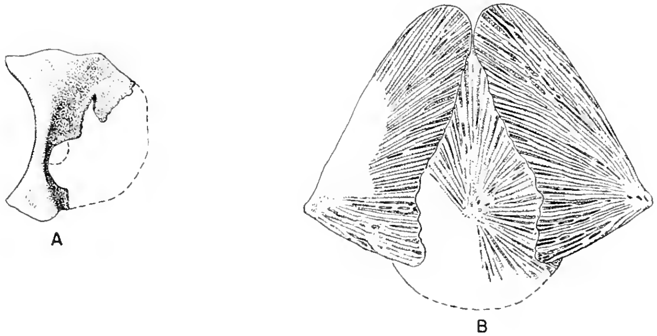

FIG. 11. Pectoral girdle of *Neldasaurus wrightae,* MCZ 2200. A, left scapulocoracoid in medial aspect, × .75. B, restoration of the dermal pectoral girdle, × .375.

The greatest width of the dermal clavicular girdle nearly equals the width of the skull. The clavicle has a roughly triangular outline. Its medial border is irregular but essentially straight; the posterior border is more or less transverse but slants diagonally forward and outward in normal position. The width of the clavicle across the base is 4.4 cm; its length is approximately 8.8 cm. A similar ratio obtains in MCZ 1371. There is a modest medial projection of the posteromedial corner of the bone. The lateral border curves inward anteriorly, but this curvature is not as pronounced as it is in such trimerorhachids as *Trimerorhachis* or *Acroplous* (Hotton, 1959). The outline in general closely resembles that of *Buettneria* (Case, 1922).

The lateral edge of the clavicle is curved upward throughout most of its length. About 3 cm anterior to the posterolateral corner of the bone, the upturned lateral edge thickens and rises, forming a stout ridge, the base of the scapular process, which increases in height posteriorly. The dorsal tip of this process is missing.

Although the interclavicle is obscured ventrally in MCZ 2200, its dorsal surface in that specimen and the portion preserved in MCZ 1371 show that it is a sizable element with a length somewhat greater than that of the clavicles. Its posterior end is bluntly truncated and extends only a short distance beyond the posterior borders of the clavicles. Anteriorly its ventral exposure is reduced by the converging medial edges of the clavicles, whose anterior ends seem to meet in front of it. An unsculptured, but striated flange of bone projects from the anterolateral edge of the interclavicle to provide a surface for the reception of the ventrally overlapping edge of the clavicle.

The ventral surfaces of the clavicles and the interclavicle have a sculpture consisting of prominent ridges and grooves radiating from centers in the respective bones. The center of the sculpture in the clavicle is near the posterolateral corner, that in the interclavicle is in the midline about a quarter of the distance forward from the posterior end. The sculpture is reticulate near the center of ossification, but rapidly becomes linear as it radiates from the center, particularly in the clavicle. The linear aspect of the sculpture is strongly developed, and anastomoses between adjacent ridges are less evident than in the thoracic girdle of *Trimerorhachis.* No cleithrum has been found.

The only trace of the endochondral shoulder girdle is a damaged left scapulocoracoid in MCZ 2200 (Fig. 11, A). The anterior margin is incomplete and a large part of the central region is missing. The general shape of the remaining portion is remarkably similar to the scapulocoracoid of *Trimerorhachis* (Williston, 1915, fig. 5, B, C, D; Case, 1935, figs. 15 and 16), and the missing portions have been restored by reference to that form as well as by continuation of the contours suggested by the broken edges of the bone.

The scapulocoracoid of *Neldasaurus* consists of an expanded blade above the articular surface of the glenoid region. In lateral view the anterior border as restored has a convex outline and the outline of the posterior border is strongly concave dorsally, less so ventrally. The bone as preserved is 3 cm high and its greatest anteroposterior extent was presumably about 2.5 cm. Thus, correlated with the flat body of *Neldasaurus,* it is proportionately shorter than the scapulocoracoid of a form like *Eryops.* The dorsal and ventral edges are unfinished and were presumably continued by cartilage. The thickness of the edges of the bone as preserved suggests that the anterior edge was thinner than the dorsal and posterior margins.

The posterior margin is thickened and rounded, the lower two-thirds being confluent with a modest vertical ridge on the medial side of the bone above the articular surface of the glenoid region. Anterior to this ridge the posterior portion of the scapular blade is pierced by an oval supraglenoid foramen about one-third of the way above the base.

Although the general form of the scapulocoracoid of *Neldasaurus* is strikingly similar to that of *Trimerorhachis* there are marked differences in proportion. Where the scapulocoracoid of *Trimerorhachis* is short and stocky, in *Neldasaurus* it is lightly constructed, taller and thinner; the articular area of the base is only half as large as that area in *Trimerorhachis*. The vertical ridge above the articular surface in *Trimerorhachis* is separated from the thickened posterior margin of the bone, whereas in *Neldasaurus* it is confluent with the posterior margin.

Anterior Limb (Figure 12). A partial left forelimb and manus are preserved in MCZ 1371 (Pl. 5). The manus as preserved has four metacarpals, with two phalanges articulated with the third and one with the fourth. The carpus was not preserved and was presumably unossified.

There is an incomplete, disarticulated right forelimb in MCZ 2200.

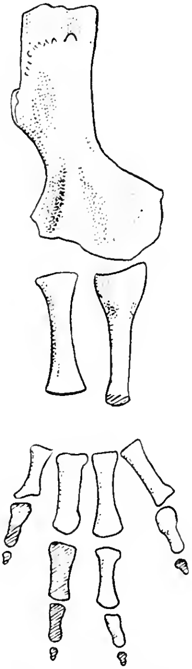

FIG. 12. *Neldasaurus wrightae.* Left anterior limb restored from MCZ 2200 and MCZ 1371, × .75. Restored areas are hatched.

Partial humeri associated with MCZ 2516, 2518, and 2406 show some surfaces not visible in the specimens described above.

The reconstruction of the left forelimb of *Neldasaurus* is based mainly on MCZ 1371 with the proximal end of the ulna added from MCZ 2200. As can be seen from Plate 5, some re-orientation is necessary to put the elements in good articulation.

The forelimb is small for an animal the size of *Neldasaurus*. The humerus, which is relatively long, is of the type seen in *Trimerorhachis*. It is about 4.5 cm long and shows some development of a shaft region. The width of the distal end is 2.3 cm; the proximal end is only 1.2 cm wide. The ends are "twisted" so that the planes of their surfaces form an angle of 27 degrees. There is a well developed deltoid crest on the radial edge of the humerus, just above the middle of the bone, from which an unfinished area along the radial border reaches nearly to the proximal articular surface. There is a small process .5 cm below the top of the humerus on the lateral face as seen in MCZ 2518. In the normally oriented limb its position is near the posterior edge and it probably represents the processus latissmus dorsi. The deltoid crest and this process are connected by a curved band of short, radial striations, presumably supplying part of the deltopectoral insertion. The entepicondyle is strongly developed. The supinator process is continuous with a ridge which projects beyond the ectepicondyle on the distal radial margin of the bone.

The radius is a short, stout bone, about 2.2 cm long, and expanded at both ends. In end view the proximal end is nearly circular, the distal end more like a flattened oval. The bone is not evenly rounded, and what appears to be the medial surface is rather sharply separated from a lateral-anterior surface by a pronounced longitudinal ridge. The side of the shaft opposed to the ulna is concave.

The ulna is slightly longer than the radius, as would be expected, though the exact length cannot be determined. The shaft is curved and very narrow. The proximal end is strongly expanded. The distal end is only slightly expanded. A ridge, similar to that seen in the ulna of *Trimerorhachis*, occurs on the inner posterior border of the proximal end of the bone.

The articular ends of the bones described above are unfinished and excavated, indicating that they were originally capped by cartilage.

The manus was preserved in lateral aspect. The limb bones on the slab are seen from the medial aspect and must be turned over to agree with the position of the manus. This move correctly places the radius above the first metacarpal.

There are four digits in the manus. The phalangeal count as restored is 2.3.3.2. The metacarpals are relatively long, slender bones and have a flattened-oval outline in cross section. The two central metacarpals are the longest. The first metacarpal, on the radial side of the manus, is the shortest, and is only a little more than half as long as the second and third. The fourth metacarpal is smaller than the middle two but larger than the first. The phalanges as preserved are slender bones, with the articular swelling at the distal end less pronounced than that at the proximal end. In both metacarpals and phalanges, as is fairly common, most distal articular surfaces are convex, whereas the proximal articulations are flattened.

The pectoral limb of *Neldasaurus* is strikingly similar to that of *Trimerorhachis*. It would be difficult, if not impossible, to distinguish between individual bones of the two forms. As can be seen in Case's reconstruction (Case, 1935, fig. 26, p. 267), the restored manus of *Neldasaurus* matches that of *Trimerorhachis*.[1]

Pelvic Girdle (Figure 13). MCZ 2518 contains the only pelvic girdle material. There are two ilia with this specimen. The left ilium is seen from the medial side. The lower part of the right ilium is separated from the blade, which is in the same block, and can be seen both medially and laterally. There are no remains of pubis or ischium.

The height of the ilium is approximately 3.3 cm; the expanded base is 2 cm across. The iliac blade, slender but expanded distally, is directed dorsally. The tip of the blade is 1.2 cm long, but its width in the middle of the shaft is only .5 cm. The slender proportions of the ilium recall the slight construction of the scapulocoracoid. The general form is similar to that of *Trimerorhachis*, but the ilium is relatively taller and more slender than in that animal. The lateral surface of the base is somewhat concave. The central portion of the base is strongly produced medially and somewhat ventrally. The upper portion of the acetabulum is located above the edge of the base in the center of the lateral concave face. The unfinished articular surface is bounded by an upraised ridge dorsally. The ventral surface of the ilium shows an unfinished, excavated area that was formerly continued in cartilage. There is no indication of an attachment area for a

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[1] Case has reversed the position of the radius and ulna in his figures.

sacral rib on the inner side of the iliac blade. The top of the iliac blade is unfinished and was presumably continued in cartilage.

Posterior Limb (Figure 13). Pelvic limb material is fragmentary and poorly represented. Portions of femora include the damaged proximal and distal ends of a right femur from MCZ 2406, an incomplete shaft from MCZ 2518, a damaged distal end of a femur from MCZ 2407, and the proximal end of a small femur and the distal end of another in scrap associated with MCZ 2404. The last named elements are about half the size of those from MCZ 2406 but the structure is the same. The femur is of the peculiar *Trimerorhachis* type, with a cylindrical shaft and expanded ends. There is a shallow depression on the ventral proximal surface, bounded anteriorly by a projecting trochanter. The outer edge of the latter curves inward toward the shaft distally. The posterior margin of the depression opposite the trochanter is not strongly developed, so that the Y-shaped pattern of ventral ridges common in this area (Romer, 1947) is lacking. The adductor crest is represented by a modest, narrow ridge. Distally, this ridge ends in the center of the ventral surface, a short distance above the end of the bone. Below it,

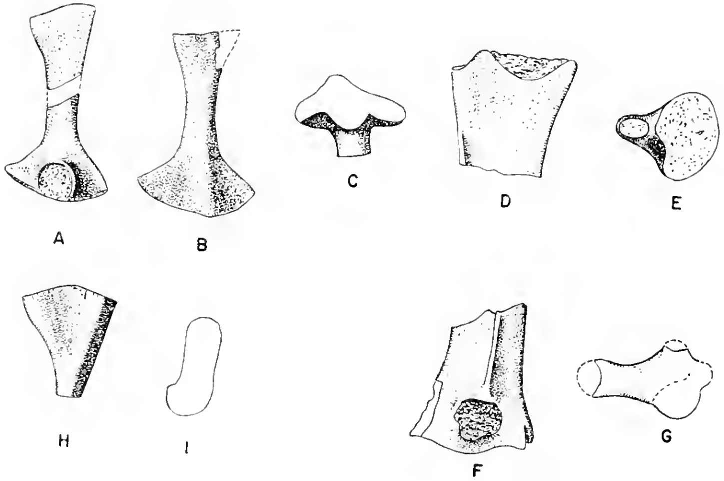

FIG. 13. Pelvic girdle and limb elements of *Neldasaurus*. A, right ilium, outer side. B, left ilium, inner side. C, right ilium, distal surface. A-C, MCZ 2518, × .75 approx. D and E, ventral and proximal views of proximal end of femur. F and G, ventral and distal views of distal end of femur. D-G, MCZ 2406, × 1.5 approx. H and I, inner and proximal view of proximal end of a right tibia of MCZ 2404, × .75 approx.

centrally, is a popliteal space. In MCZ 2407 this is a smooth depression, but in MCZ 2406 it is a rugose, unfinished surface, bounded dorsally by a low upraised ridge. The distal end of the femur has a double condylar area for the head of the tibia and a smaller, lateral condyle for the fibula.

The lower limb bones are represented by the proximal portion of a right tibia and the distal end of a fibula from MCZ 2404, and a similar fragment of fibula from MCZ 2407. The proximal end of the tibia is massive and there is a well developed cnemial crest. The bone tapers rapidly to a slender shaft below the head. The width of the proximal end is 1.7 cm, while the shaft, which is oval in cross section, is only 5 mm across (Fig. 13, H and I).

The fragment assigned to the fibula shows a sub-oval shaft, below which the distal end is considerably expanded, though flattened. Identification of this bone is uncertain.

As far as known, the posterior limb bones of *Neldasaurus* are indistinguishable from those of *Trimerorhachis,* with the possible exception of the distal end of the femur of MCZ 2406. Review of the *Trimerorhachis* material in the collection of the Museum of Comparative Zoology failed to uncover any femora with the peculiar popliteal fossa of that bone.

Assignment of these materials to *Neldasaurus* is not as certain as was the case with the pectoral limb. A single intercentrum of *Trimerorhachis*-type is present in MCZ 2404 and another in MCZ 2406. MCZ 2516 contains two small *Trimerorhachis*-like intercentra and a pleurocentrum. However, all of these specimens are from the Moran formation, from which there has been no definite evidence of the occurrence of *Trimerorhachis* (Olson, 1955). Most of the materials included in the specimens listed here are *Neldasaurus*-like, and the limb materials described compare favorably in size with the other *Neldasaurus* elements in these specimens. For this reason, and because the few *Trimerorhachis*-like vertebral elements do not seem sufficient evidence on which to establish the presence of that animal in the Moran, reference of the posterior limb elements to *Neldasaurus* seems reasonable.

SCALES

Remnants of dermal armor consisting of thin, imbricated bony scales are preserved in a number of places in the specimens. Isolated patches of integumental material are present in MCZ 2200 and MCZ 2518, and in MCZ 1371 considerable areas are preserved. The pattern of scale distribution is obscure, but the occurrence of scale material in association with much of the skeleton suggests that scales covered most of the dorsal surface of the body.

Scale structure and arrangement is best seen in MCZ 1371 (Fig. 14). In most cases the dermal covering as preserved consists of groups of small, parallel bony rods, the longest about 1 cm long, covering all parts of the skeleton with the exception of the skull and dermal shoulder girdle. Isolated patches of rods were found on the posterior portions of the clavicles and interclavicle but their separation from the main mass of integumental material suggests post-mortem displacement. In a number of areas the integument appears to have contained as many as seven layers of bony rods, one above the other. This condition is similar to that of the layers of "bony fibrillae" described by Williston (1916) in *Trimerorhachis.*

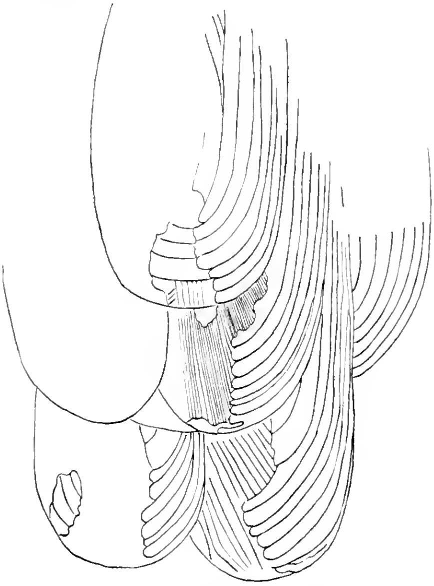

FIG. 14. Dermal scales of *Neldasaurus wrightae,* MCZ 1371, × 5.

More or less complete scales are seen in only a few places. The scales are elongate and rounded at both ends. As near as can be determined, they are 10-12 mm long and 4-5 mm wide, and, as shown by their layered condition, overlapped to a considerable degree. However, they are very thin, and even in areas where they are in several layers they easily conform to the contours of the underlying skeleton. Colbert (1955) has shown that the "bony fibrillae" described by Williston were in fact remnants of elongate bony scales in *Trimerorhachis*. Comparison of the scales of *Neldasaurus* with the scales of *Trimerorhachis* from the specimens on which Colbert based his paper shows the squamation of the two forms to be alike. As in *Trimerorhachis,* some scales have a superficial layer of fine longitudinal striations, below which is a layer of bony rods of variable width arranged in concentric rings. The presence of the superficial layer, however, is rare in *Neldasaurus* specimens.

OTHER OCCURRENCES OF *NELDASAURUS*

Fragmentary remains of small rhachitomous amphibians have been recovered from several Dunkard localities in West Virginia (Romer, 1952). Early collections of some of these were referred to *Trimerorhachis* (Whipple and Case, 1930; Tilton, 1926). Romer (1952), noting the absence of proof of the existence of *Trimerorhachis* in these beds, described a series of vertebrae from these collections, comparing them with "a rhachitome from the lower Wichita formations (Putnam, Moran) of Texas" in reference to the then undescribed *Neldasaurus*. Comparison of an isolated intercentrum from locality 28 in the Greene Group and an articulated series of three vertebrae from locality 4 of the Washington Group of West Virginia (Moran, 1952; Romer, 1952) (Carnegie Museum nos. 8568 and 8569) has been made with comparable elements for *Neldasaurus*. These elements, (see Romer, 1952, fig. 2, p. 65 and pl. 2, figs. 3 and 4) are remarkably similar to those of *Neldasaurus*, particularly in the height of the pleurocentra and narrow dimensions of the ascending processes of the intercentra.

Hotton (1959) compared vertebral elements of *Acroplous* with those described by Romer, along with some other material from the Dunkard region, finding an isolated parasphenoid and the vertebral elements to bear a close resemblance to those of *Acroplous.*

Correlation of the continental deposits of the Dunkard with Texas beds is somewhat uncertain, but it is generally assumed that the Washington and Greene Groups of the Dunkard are equivalent in age to the Wichita in Texas (Romer, 1958) and represent the base of the Lower Permian in that region. Further, Romer (1952) has demonstrated a general similarity in the faunal assemblages of the Dunkard and the Lower Permian redbeds of Texas.

On the basis of the resemblance of the circumchordal elements of *Neldasaurus* and the Dunkard specimens, and the approximate correlation of the Texas and West Virginia beds, there is a strong likelihood that *Neldasaurus* (and/or *Acroplous*) or some closely related form was present in the Dunkard.

DISCUSSION

Comparison of *Neldasaurus* with other Genera of Trimerorhachoids

The description of this new genus, obviously comparable in many ways to *Trimerorhachis,* suggests the advisability of a general review of the trimerorhachoids — the membership of this group of labyrinthodonts, their structural patterns, classification and relationships. To this end, the first portion of the discussion consists of a morphological comparison of *Neldasaurus* with the other trimerorhachoid genera.

Animals which have been suggested by various authors as belonging to the trimerorhachoid complex include, *Trimerorhachis, Saurerpeton, Eobrachyops, Acroplous, Dvinosaurus, Chalcosaurus, Slaugenhopia, Eugyrinus* and other "peliontids," and *Dawsonia.* Although the entire group is reviewed, detailed comparisons are confined to those genera about whose structure we have sufficient knowledge.

Before proceeding with individual comparisons, we may note that the elongate snout of *Neldasaurus* is sharply contrasted to the abbreviated snout of other members of the group. Other features apparently related to snout proportions in which *Neldasaurus* differs from typical trimerorhachoids include elongation of the dermal bones of the face and palate, failure of the lacrimal to reach the naris, and broad separation of the choanae from the interpterygoid vacuities.

Neldasaurus and Trimerorhachis (Fig. 15). It is obvious from the description given that *Neldasaurus,* apart from facial length, has the combination of primitive and advanced characters seen in the Trimerorhachoidea, as this term is used by Romer. Further, except in this one feature, *Neldasaurus* is obviously closely related to *Trimerorhachis* and will fit into the family

Trimerorhachidae (Romer, 1947, p. 312). *Trimerorhachis* is a well known form from the Texas redbeds whose anatomy has been described by Cope (1878), Broom (1913), Williston (1915, 1916), Case (1911, 1935), and Watson (1956).

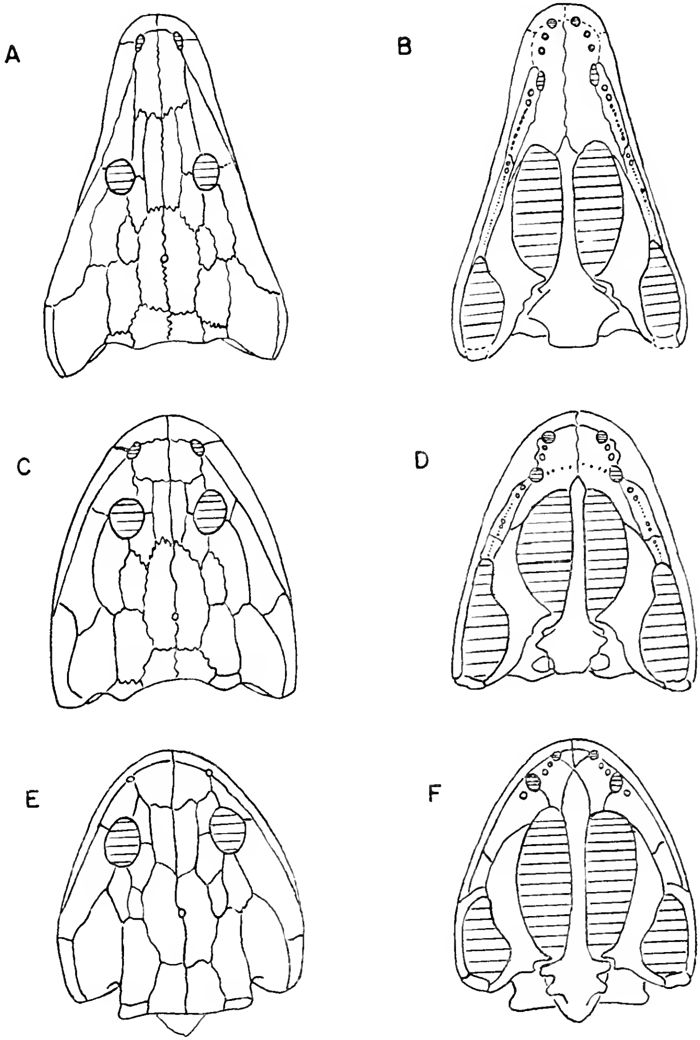

FIG. 15. Trimerorhachid skulls reduced to the same width. Dorsal and palatal views of A-B, *Neldasaurus;* C-D *Trimerorhachis* after Case; E-F, *Saurerpeton* after Romer and Watson.

In addition to the resemblances between *Neldasaurus* and *Trimerorhachis* related to general level of organization, the two show numerous close resemblances of a special nature. The skulls are alike in such features as the general pattern of dermal bones, narrow interorbital width, prominent sensory canal grooves, relation of the anterior palatal bones to the interpterygoid vacuities, symphysial tusks and anterior palatal fenestrae, and the remarkably similar basicranial articulation. The lower jaws are similar, each having a modest retroarticular process and neither showing a coronoid process. The postcranial skeletons of *Neldasaurus* and *Trimerorhachis* are much alike and the limb bones, as noted, are nearly identical.

In spite of their close resemblance, there are a number of significant differences between *Neldasaurus* and *Trimerorhachis* other than those related to snout proportions. In some respects *Neldasaurus* seems to be somewhat more primitive than *Trimerorhachis*. Here, in contrast to *Trimerorhachis,* a low ridge bounds the skull table laterally, the skull is deeper posteriorly, the jugal enters the orbital border, and a tusk pair persists on the ectopterygoid.

Neldasaurus and *Trimerorhachis* also differ in several special characters. Prootic, opisthotic and basisphenoid elements, as far as known, were persistently cartilaginous in *Neldasaurus,* whereas in *Trimerorhachis* they were ossified. The pattern of sensory canal grooves in *Neldasaurus* differs from that of *Trimerorhachis* in failure of the supraorbital groove to enter the lacrimal and in the presence of a jugal sulcus, unknown in *Trimerorhachis.* The lateral border of the choana in *Neldasaurus* is formed by an anterior extension of the palatine. In *Trimerorhachis* it is formed in more "normal" fashion by the maxilla. Separation of the posterior wall of the "conical recess" from the anterior wall of the "excavatio tympanica" by a groove in the medial surface of the pterygoid in *Neldasaurus* is not shown by *Trimerorhachis. Neldasaurus,* with a remarkably high tooth count, has twice as many marginal upper jaw teeth as *Trimerorhachis* — about 108 as contrasted to 50. The dentary also bears more teeth in *Neldasaurus* than in *Trimerorhachis* — the approximate count being 60 and 43 respectively. This may in part be related to snout elongation in *Neldasaurus*, but tooth number is not necessarily correlated with snout length in labyrinthodonts (Chase, 1963).

A notable difference in the proportions of pleurocentra and intercentra is seen in the vertebral columns of *Neldasaurus* and *Trimerorhachis.*

SAURERPETON (Fig. 15). This small trimerorhachoid, known mainly from the Upper Pennsylvanian of Linton, Ohio, has been suggested as being closely related to *Trimerorhachis* (Romer, 1947). Romer further believed that "*Pelion lyelli,*" also from Linton, was a trimerorhachoid and erected a family Peliontidae within the Trimerorhachoidea for its reception. However, recent studies by Baird and Carroll (Carroll, 1964) show that the type of "*Pelion*" is actually a primitive dissorophid of the genus *Amphibamus,* and that the characters which Romer gave to the "Peliontidae" actually pertain to *Saurerpeton.* All other Linton specimens with an intertemporal previously described as "*Pelion,*" and "*Branchiosauravus*" (Romer, 1930) as well, apparently belong to *Saurerpeton.*

Saurerpeton shows definite trimerorhachoid characters although these are generally developed to a lesser degree than in *Neldasaurus* and *Trimerorhachis.* It also resembles them in such special characters as sensory canal grooves on at least some of the dermal roof bones, and anterior palatal fenestrae for the reception of symphysial tusks. These openings are clearly shown in Romer's "*Pelion*" (1930), though Steen (1931) and Watson (1956) reconstruct "*Pelion*" without anterior palatal fenestrae. It appears from Steen's figure 15 of "*Pelion lyelli*" Wyman that the prevomers are displaced from right to left so that, as Romer (1947) suggests, she has interpreted the anterior palatal fenestrae as the choanae. In this she is followed by Watson. In some *Saurerpeton* specimens (Romer, 1930, fig. 6) it appears that the palatine nearly reaches the prevomer lateral to the choana, a feature suggestive of the pattern in *Neldasaurus.*

Saurerpeton resembles *Trimerorhachis* more than *Neldasaurus* in such features as the proportions of the antorbital region and in the small ectopterygoid in the palate.

In the retention of three palatal tusk pairs, *Saurerpeton* resembles *Neldasaurus* rather than *Trimerorhachis.*

In several significant features *Saurerpeton* differs from *Neldasaurus* and *Trimerorhachis,* and in part, in keeping with its greater age, it is seemingly more primitive. In *Saurerpeton* the otic notch, though reduced, is more highly developed than in *Neldasaurus* and *Trimerorhachis.* The orbits in *Saurerpeton* are widely spaced and the jugal forms most of the lateral orbital border. The skull in *Saurerpeton* appears to be deeper than in *Neldasaurus* and *Trimerorhachis.* Watson (1956) estimates a width to height skull ratio in "*Pelion*" of 1:1. The ratio in *Neldasaurus* is 3:1 and in *Trimerorhachis* (Watson, 1956) it is

4.4:1. *Saurerpeton* has fewer marginal upper jaw teeth (about 38) than *Neldasaurus* and *Trimerorhachis* and also lacks the large number of small palatal teeth seen in them.

Saurerpeton differs from *Neldasaurus* and *Trimerorhachis* in several special characters as follows:

(1) The occiput projects posteriorly beyond the skull table.
(2) The quadrate condyle appears to have been somewhat anterior to the occipital condyle and well below the level of the floor of the braincase.
(3) The tabulars are remarkably small.
(4) The palatine enters the border of the interpterygoid vacuity between the vomer and the pterygoid.
(5) The maxilla is truncated posteriorly and does not reach the subtemporal fossa.
(6) The quadrate ramus of the pterygoid is short and has a vertical, ventrally directed flange laterally.
(7) There is a coronoid process in the lower jaw.

The very long skull table in *Saurerpeton* is a remarkable feature (Romer, 1947), and both supratemporal and squamosal share in the elongation to an extent not seen in *Neldasaurus* and *Trimerorhachis*.

Eobrachyops (Fig. 16). This genus has been described by Watson (1956) on the basis of a specimen from the Lower Permian of Texas. There is no preserved record concerning the collection of the specimen, but the matrix strongly suggests the Clear Fork and, since no materials of that group from higher levels were collected before Olson's recent work, it is highly probable that *Eobrachyops* comes from the Arroyo Formation. Watson's specimen lacked the anterior end of both palate and lower jaw. *Eobrachyops* resembles other trimerorhachoids in its general level of organization and can readily be admitted to the Trimerorhachoidea by accepting Hotton's modification of Romer's definition of the superfamily to include the phrase, "otic notch often poorly developed or lacking" (Hotton, 1959).

Eobrachyops differs from *Neldasaurus, Trimerorhachis* and *Saurerpeton* in some special characters. It apparently had an ossified supraoccipital; the lacrimal is confined to the orbital region, its usual area being provided for by an enlarged septomaxilla; the prefrontal reaches from orbit to naris; sensory canal grooves are essentially confined to circumorbital rings.

In some ways *Eobrachyops* appears to be advanced beyond the level of the other animals so far considered. The exoccipitals are expanded, enclosing the vagal foramen and meeting the tabulars, thus sheathing posteriorly the cartilaginous paroccipital. Sphenethmoid and quadrate, as well as the prootic elements, are unossified. The interpterygoid vacuities are larger than in

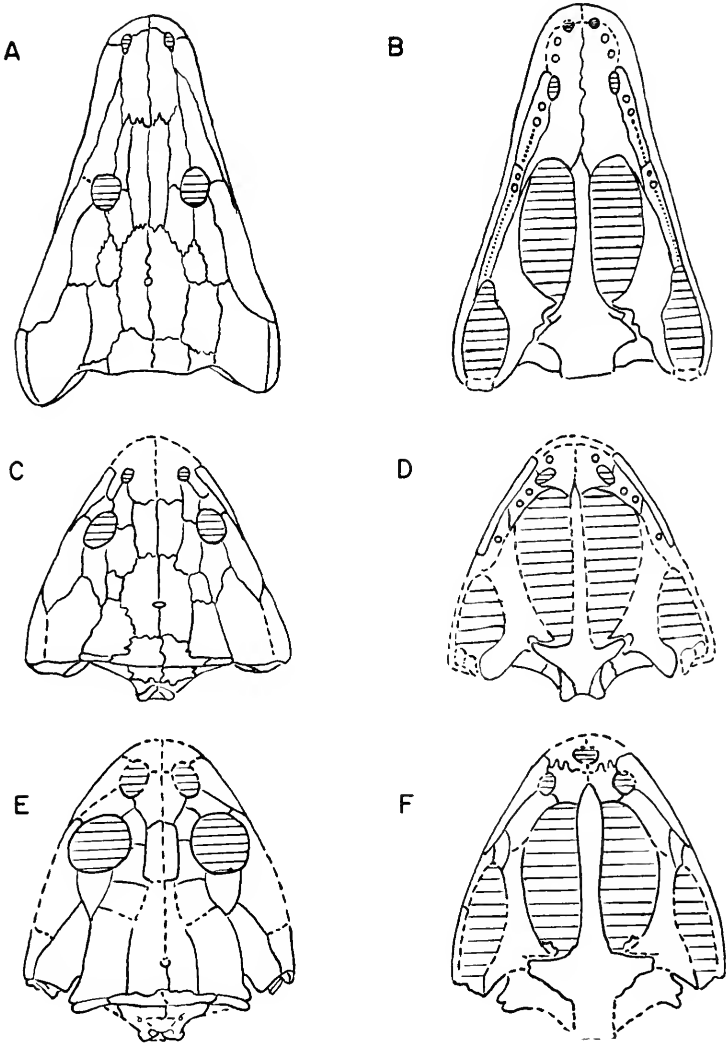

Fig. 16. Trimerorhachid skulls reduced to the same width. Dorsal and palatal views of A-B, *Neldasaurus*; C-D, *Eobrachyops* after Watson; E-F, *Acroplous* after Hotton.

the previously discussed trimerorhachoids, being separated from the choanae only by a narrow strip of bone. The tabulars are reduced to narrow strips. There is no otic notch.

Eobrachyops resembles *Neldasaurus* in two important skull features not shared by other trimerorhachoids. The elongate ectopterygoid and the unusual palatine-vomer union lateral to the choana suggest a real relationship between them.

On the other hand, *Eobrachyops* resembles *Saurerpeton* rather than *Neldasaurus* and *Trimerorhachis* in the seven characters listed above (p. 210). Further, we can add to this list of resemblances: (8) Jugal contact with the orbital border broad. (9) Skull deep posteriorly. Also, *Eobrachyops,* like *Saurerpeton,* has widely-spaced orbits.

The proportions of intercentra and pleurocentra in *Eobrachyops* are like those of *Neldasaurus* and are contrasted to those of *Trimerorhachis.* Conditions in *Saurerpeton* are uncertain.

Acroplous (Fig. 16). This genus, recently described by Hotton (1959), comes from the Speiser Formation, Council Grove Group of the Wolfcamp series of Kansas. According to correlation tables of Permian formations in North America (Dunbar et al., 1960), this level is approximately equivalent to that of the Putnam Formation of the Wichita in Texas. Hence, *Acroplous* was a contemporary of *Neldasaurus* and *Trimerorhachis. Acroplous* is a highly specialized form with an extremely short face, in which the dermal bones are crowded by large, dorsally situated nares. However, *Acroplous* has all of the important trimerorhachoid characters.

In some characters *Acroplous* resembles one or another of the animals previously considered. The slit-like otic notch in *Acroplous* suggests a primitive condition and most nearly resembles that of *Saurerpeton.* The small ectopterygoid is like that seen in *Saurerpeton* and *Trimerorhachis.* The lack of an ossified quadrate and sphenethmoid in *Acroplous,* as well as the presence of an ossified supraoccipital, recalls conditions in *Eobrachyops.* Also, as in *Eobrachyops,* the tabulars are strip-like, and the sensory canal grooves are confined to the orbit region.

Most significant is the fact that *Acroplous* resembles *Eobrachyops* and *Saurerpeton* in the nine important characters listed above, which distinguish the last two animals from *Neldasaurus* and *Trimerorhachis.*

The proportions of the intercentra and pleurocentra of *Acroplous* resemble those of *Neldasaurus* and *Eobrachyops.*

DVINOSAURUS. This perennibranchiate labyrinthodont of the Russian Upper Permian has been described by Amalitsky (1924), Sushkin (1936), and Bystrow (1938). *Dvinosaurus* has a short face, anteriorly placed orbits, a very short skull, and lacks an intertemporal element. Some of these characters may be associated with "larval tendencies."

Dvinosaurus shows resemblance to the earlier trimerorhachoids in almost every feature. The only notable exceptions are the apparent lack of the intertemporal and — most important — the shortness of the skull as a whole. Bystrow suggests a probably compound nature of the postorbital — the posteromedial portion of the bone representing a fused intertemporal moiety. The absence of a discrete intertemporal is, therefore, no bar to trimerorhachoid relationship for *Dvinosaurus*. Further, though the skull is short, even here the proportions of pre- and postorbital segments are those of trimerorhachoids, and the general shortness can be attributed to neoteny, since it is known in several cases that the skull of larval labyrinthodonts is proportionately much shorter than in the adult.

Dvinosaurus is set apart from other trimerorhachoids by certain special characters, such as enclosure of the quadrate foramen by the quadratojugal, a greatly reduced palatine, a somewhat specialized palatal dentition, and a long-stemmed interclavicle. Further, it shows several advanced characters, as might be expected in a late-surviving trimerorhachoid. In two skull features — an essentially double occipital condyle and a tabular process which forms the outer end of the paroccipital bar — *Dvinosaurus* is advanced over all other trimerorhachoids. The exoccipitals in *Dvinosaurus* are expanded to surround the vagal foramen, a feature in which *Dvinosaurus* is more advanced than other members of this group with the exception of *Eobrachyops*. The degree of ossification in *Dvinosaurus*, in which the otic elements and the sphenethmoid remain cartilaginous while a small ossified supraoccipital occurs in at least some specimens, recalls conditions in *Acroplous* and *Eobrachyops*. *Dvinosaurus* also has an unossified gap between the posterior end of the quadrate ramus of the pterygoid and the squamosal (Bystrow's "pterygosquamosal fissure"). A similar condition obtains in *Eobrachyops* but in no other trimerorhachoid.

In several characters *Dvinosaurus* seems to resemble *Saurerpeton*, *Acroplous* and *Eobrachyops* rather than *Neldasaurus* and *Trimerorhachis*, although in *Dvinosaurus* these characters are generally developed to a lesser degree. In *Dvinosaurus* the occiput projects behind the skull table, the quadrate condyle is about even with or slightly in advance of the level of the occipital condyle and lies below the level of the ventral surface of the parasphenoid, the pterygoid has a ventral flange laterally, the jugal has a broad contact with the orbital border, the orbits are wide-spaced, and there is a coronoid process in the lower jaw.

Although the skull of *Dvinosaurus* is deepened posteriorly, it is considerably flatter than in *Saurerpeton, Acroplous* or *Eobrachyops.* Furthermore, *Dvinosaurus* resembles *Neldasaurus* and *Trimerorhachis* and is in contrast to the other three animals in several important characters. In *Dvinosaurus* the otic notch is reduced and is essentially comparable to the otic notch in *Neldasaurus* and *Trimerorhachis.* The tabular is small, though it is not reduced to a narrow strip. The pattern of the sensory canal grooves on the dermal roof bones of *Dvinosaurus* closely resembles that of *Trimerorhachis* and is nearly identical to that of *Neldasaurus.*

In *Dvinosaurus,* as in *Neldasaurus* and *Trimerorhachis,* there is a union of the vomer and the palatine in the palate, and the maxilla is not truncated posteriorly but reaches the anterior end of the subtemporal fossa.

The vertebral elements of *Dvinosaurus* are most like those of *Trimerorhachis.*

Chalcosaurus. This poorly known labyrinthodont was tentatively assigned to the Trimerorhachidae by Romer (1947). The original specimen has been lost, but Efremov redescribed the genus on the basis of the literature and published a figure (1940, pl. II, fig. 2). On the basis of the description, assignment of *Chalcosaurus* to the trimerorhachid group seems reasonable, but knowledge of this animal is too scanty to permit definitive comparisons.

Slaugenhopia. This genus, recently described by Olson (1962), is based on partial skull material from the San Angelo of Texas and a partial lower jaw from the same horizon (Olson and Beerbower, 1953). The incomplete nature of the remains precludes definitive discussion and we here provisionally accept Olson's assignment of *Slaugenhopia* to the Trimerorhachidae.

Eugyrinus. This small, short-faced genus from the Pennsylvanian Coal Measures in Lancashire has been described by Woodward (1891), and by Watson (1921, 1940), and its phylogenetic position has been considered by Romer (1947). Romer assigned it to the "Peliontidae," a group now known to be unreal, and considered it a young, though probably post-larval member of the primitive rhachitome group. Further, Watson (1940) has compared *Eugyrinus* with *Dendrerpeton*. More recent unpublished studies by Carroll indicate that *Eugyrinus* is more closely allied to the edopsoids than to the trimerorhachoids, and should probably be removed from the trimerorhachoid complex and placed near the base of the edopsoid group. Hence, *Eugyrinus* is not here considered as a trimerorhachoid.

OTHER "PELIONTIDS." Included tentatively in Romer's family Peliontidae with "*Pelion*" and *Eugyrinus* were *Erpetocephalus* and various Mazon Creek "larvae."

The position of *Erpetocephalus* is problematical. Aside from traces of shoulder girdle, only the dorsal surface of the head is known (Romer, 1947). According to Baird (*in litteris*), "*Erpetocephalus* is a labyrinthodont of uncertain position; Romer (1945) very plausibly classified it as a dendrerpetontid edopsoid." There seems to be no strong argument for assigning it to the trimerorhachoid complex.

Baird's studies have further shown that the Mazon Creek larvae are either indeterminate or that they are not trimerorhachoids.

DAWSONIA POLYDENS was based on a number of fragmentary remains of Carboniferous age (Fritsch, 1901). Romer (1945) reviewed the material, finding identification uncertain. Figures (Fritsch, 1901, vol. 1, figs. 42, 43) and copper casts of the original specimens support the assumption that we are here dealing with a primitive temnospondyl of indeterminate affinities.

INTERRELATIONSHIPS OF TRIMERORHACHOID GENERA

The genera here considered trimerorhachoids, in spite of many variations in structure, share a large number of characters related to their general level of organization. The resemblances that in combination suggest the Trimerorhachoidea to have been a natural group are:

(1) Presence of an intertemporal element — the compound nature of the postorbital in *Dvinosaurus* justifies its inclusion here.
(2) Single occipital condyle — the condyle tending towards a double condition in *Dvinosaurus;* conditions in *Acroplous* are incompletely known.
(3) A movable basal articulation.

(4) Tendency towards flattening of the skull, at least in the antorbital region.
(5) Otic notch small, poorly developed or lacking.
(6) Postorbital segment of the skull expanded.
(7) Usually short-faced — *Neldasaurus* is the only exception.
(8) Quadrate close to the level of the occipital condyle.
(9) Presence of sensory canal grooves on the dermal roof bones, often well developed.
(10) Interpterygoid vacuities enlarged.
(11) Broad cultriform process of the parasphenoid.
(12) Anterior palatal fenestrae and symphysial tusks, where known.
(13) A modest retroarticular process in the lower jaw.
(14) Ventral dermal shoulder girdle expanded.
(15) Body flattened.
(16) Limbs small.

Phylogenetic relationships and classification of the trimerorhachoids have been recently treated, principally by Romer (1947), Watson (1956), and Hotton (1959), with varying results. The description of *Neldasaurus* and the discussion of trimerorhachoids in the last section provide an opportunity to review relationships within the group.

Neldasaurus resembles *Trimerorhachis* more closely than any other trimerorhachoid. However, these animals differ in special characters, some of advanced nature, which indicate that the relationship between them is probably not an ancestor-descendant one. Their typically trimerorhachoid features and their appearance near the base of the Permian suggest that they probably arose from a trimerorhachoid ancestor in the Pennsylvanian. *Saurerpeton* has been suggested as being closely related to the ancestry of *Trimerorhachis* by Romer (1947) and Hotton (1959). Several primitive features in *Saurerpeton* anticipate conditions in *Neldasaurus* and *Trimerorhachis*. However, some characters, e.g. the anterior position of the quadrate condyle, and failure of the pterygoids to meet the vomers, suggest that *Saurerpeton* has already advanced beyond the evolutionary stage represented by *Neldasaurus* and *Trimerorhachis*. We are thus led to the conclusion that *Saurerpeton*, though close to the ancestry of *Neldasaurus* and *Trimerorhachis*, is not directly ancestral to them.

Eobrachyops, though sharing some special characters with *Neldasaurus* and *Trimerorhachis*, shares a long list of important characters with *Saurerpeton* which are in contrast to conditions in *Neldasaurus* and *Trimerorhachis*. The combination of primitive and special characters shown by *Saurerpeton* would logically place it close to the ancestry of *Eobrachyops*.

Acroplous has been shown to resemble *Saurerpeton* and *Eobrachyops* in characters that distinguish them from *Neldasaurus* and *Trimerorhachis*. Hotton (1959) recognized the similarity of *Acroplous* to *Eobrachyops*, but placed it closer to *Trimerorhachis* mainly on the basis of three characters. These were:

(1) The presence of narrow midline elements in *Acroplous* and *Trimerorhachis*.

(2) Symphysial tusks and anterior palatal fenestrae in *Acroplous* and *Trimerorhachis*.

(3) The "normal" pattern of palatal bones adjacent to the choana in *Acroplous* and *Trimerorhachis*, as opposed to the "peculiar" situation in *Eobrachyops*, where the palatine provides the lateral boundary of the choana.

A review of these differences suggests that they may not support closer relationship of *Acroplous* to *Trimerorhachis* than to *Eobrachyops*.

(1) The narrow midline elements in *Trimerorhachis*, as well as in *Neldasaurus*, appear to result from a medial shift in the position of the orbits. In primitive temnospondyls the orbits are widely separated, the postorbital is confined to the posterior border of the orbit and the jugal forms much of the lateral border. With a medial shift in position, the orbit would, in effect, "move away" from the jugal, the postorbital would have a more lateral position relative to the orbit and by an anterior extension could replace (cf. *Trimerorhachis*) or nearly replace (cf. *Neldasaurus*) the jugal on the outer orbital border; the midline elements would at the same time be constricted. In *Acroplous* the strong jugal contact with the lateral border of the orbit and the position of the postorbital immediately behind the orbit suggest that the narrow midline elements here are the result of absolute increase in size of the orbits rather than a shift in position.

(2) The anterior end of the palate and the lower jaw in *Eobrachyops* are not known, and hence we do not know whether symphysial tusks and anterior palatal fenestrae were present or not in *Eobrachyops*.

(3) The unusual union of the palatine with the vomer on the lateral border of the choana in *Eobrachyops* is a real difference between *Eobrachyops* and *Acroplous*. However, the occurrence of a similar pattern in *Neldasaurus*, as noted above, a form obviously close to *Trimerorhachis*, suggests that the "normal" pattern may have been modified in parallel fashion in *Eobrachyops* and *Neldasaurus*.

Although in many respects, as Hotton noted, *Acroplous* appears to be a morphological intermediate between *Saurerpeton* and *Eobrachyops*, special characters in *Acroplous* suggest that it probably represents a specialized side branch of the line leading from *Saurerpeton* to *Eobrachyops*.

The aberrant structure of *Dvinosaurus* appears to remove it from close relationship to any trimerorhachoid. Romer (1947) and Hotton (1959) suggested relationship of *Dvinosaurus* to *Trimerorhachis* and *Saurerpeton*; Watson (1956) placed it in the line stemming from *Eobrachyops* to the Triassic brachyopids. In spite of resemblances of *Acroplous* and *Eobrachyops* to *Dvinosaurus*, these animals are too specialized to be reasonably considered ancestral to *Dvinosaurus*. Further, *Dvinosaurus* shares with *Neldasaurus* and *Trimerorhachis* a significant number of those characters which support separation of *Neldasaurus* and *Trimerorhachis* from *Acroplous* and *Eobrachyops*. Hence, we arrive at the conclusion that, as suggested by Romer and Hotton, *Dvinosaurus* is related to *Trimerorhachis* and might reasonably be considered a terminal member of the *Trimerorhachis-Neldasaurus* group.

Review of the Trimerorhachoidea supports the assumption that they form a natural group. The superfamily can be defined by the characters listed on pages 215-216. The phylogenetic conclusions reached above suggest the existence of three subgroups within the Trimerorhachoidea. The families Trimerorhachidae and Dvinosauridae of Romer can be retained, the first including *Trimerorhachis*, *Neldasaurus*, *Chalcosaurus* and *Slaugenhopia*, the second containing *Dvinosaurus*. I propose the erection of a new family Saurerpetontidae, with *Saurerpeton* as the type genus, for the reception of *Saurerpeton*, *Acroplous* and *Eobrachyops*.

The definitions of these families are as follows (Table 2):

TABLE 2

Family Saurerpetontidae nov.	*Family Trimerorhachidae*	*Family Dvinosauridae*
Tendency towards flattening of skull mostly confined to antorbital region.	Tendency towards flattening of skull in general.	Tendency towards flattening of skull in general but more pronounced in antorbital region.
Cheek deep posteriorly; quadrate well below level of ventral surface of parasphenoid.	Cheek not deep posteriorly; quadrate on level of ventral surface of parasphenoid.	Cheek moderately deep posteriorly; quadrate below level of ventral surface of parasphenoid.
Quadrate in advance of level of occipital condyle.	Quadrate at or behind level of occipital condyle.	Quadrate at level of occipital condyle.
Occiput projecting posterior to skull table.	Occiput not notably projecting posterior to skull table.	Occiput projecting posterior to skull table, but to a lesser degree than in saurerpetontids.
Tabulars reduced to narrow strips.	Tabulars small but not reduced to narrow strips.	Tabulars small but not reduced to narrow strips.
Jugal contact with orbital border broad.	Jugal contact with orbital border brief or lacking.	Jugal contact with orbital border broad.
Palatine entering border of interpterygoid vacuity; pterygoids not meeting vomers anteriorly.	Palatine excluded from border of interpterygoid vacuity by a union of pterygoid and vomer.	Palatine excluded from the border of interpterygoid vacuity by a union of the pterygoid and vomer.
Pronounced ventrally directed flange of pterygoid bordering subtemporal fossa.	No ventrally directed flange of pterygoid bordering subtemporal fossa.	Modest ventrally directed flange of pterygoid bordering subtemporal fossa.
Maxilla truncated, not reaching level of anterior end of subtemporal fossa posteriorly.	Maxilla not truncated, reaching level of anterior end of subtemporal fossa posteriorly.	Maxilla not truncated, reaching level of anterior end of subtemporal fossa posteriorly.
Palatal tusks not usually accompanied by small palatal teeth on vomer, palatine and ectopterygoid.	Palatal tusks usually accompanied by a row of small palatal teeth on vomer, palatine and ectopterygoid.	Palatal tusks on vomer and ectopterygoid accompanied by a row of small palatal teeth.

TRIMERORHACHOID ORIGINS AND RELATIONSHIPS

The origin of the trimerorhachoids is problematical. Some characters of this group are advanced and of a sort typically met with in Triassic labyrinthodonts. On the other hand, a number of primitive features in the trimerorhachoids, notably single condyle, movable basal articulation, and retention of intertemporal, are not found in labyrinthodonts above the edopsoid level and hence suggest an origin of the trimerorhachoids from an early member of the edopsoid group.

Among the earliest edopsoids are such Pennsylvanian forms as *Gaudrya* from Nýřany, the dendrerpetontids from Joggins, and the English edopsoid-like labyrinthodont, *Eugyrinus*. A trend in dermal roof pattern in edopsoids, characterized by withdrawal of the lacrimal from the anterior orbital border, is already well established in *Gaudrya* and the dendrerpetontids, which would bar them from being directly ancestral to the trimerorhachoids.

Eugyrinus shows a number of characters that might be expected in a trimerorhachoid ancestor, such as: (a) short skull, (b) broad snout, (c) short face, (d) small otic notch, (e) skull table moderately expanded, (f) apparently single condyle, (g) parietal foramen close to orbits, (h) primitive dermal roof pattern, including intertemporal, (i) traces of lateral line grooves on dermal bones of skull roof, (j) open palate, but with pterygoids still extending anteriorly to nearly meet cultriform processes on the anteromedial edges of the interpterygoid vacuities, (k) apparently movable basal articulation, (l) lower jaw with a modest retroarticular process and coronoid process, the last named structure occurring in many, though not all trimerorhachoids.

Only in one specific point is *Eugyrinus* too specialized to be a trimerorhachoid ancestor — the fact that, unlike conditions in any trimerorhachoid, the quadratojugal enters into the jaw articulation. However, an edopsoid resembling *Eugyrinus* in all features except this one specealization would be a reasonable trimerorhachoid ancestor.

The possible relationship of trimerorhachoids to the Triassic brachyopids has been treated by Watson, Nilsson and Romer. Watson (1956) proposes *Eobrachyops* and *Drinosaurus* (1919, 1956) as ancestors of the Triassic brachyopids; *Drinosaurus*, according to that author, represents a more or less intermediate stage in a line stemming from an ancestral form close to

Eobrachyops in the Lower Permian. Nilsson (1937) agrees in general that *Drinosaurus*, though not directly ancestral, may be close to the ancestry of brachyopids. Romer (1947) denied relationship of *Drinosaurus* to the brachyopids, considering it closer to *Saurerpeton* and *Trimerorhachis*, and suggested the metoposaurs as brachyopid ancestors.

In its parabolic skull outline and anteriorly placed orbits, *Drinosaurus* superficially resembles the brachyopids. However, the pattern of dermal bones in the skull roof of *Drinosaurus*, including reduction of the postparietal and the topography of the postorbital region, is in contrast to conditions in the brachyopids where the postparietals are not notably reduced and the postfrontal-supratemporal contact, as Romer points out, is more reasonably derived from the more "normal" pattern of typical rhachitomes. Further, the lacrimal contact with the orbit and naris in *Drinosaurus* differs from the brachyopid condition, in which the lacrimal is typically reduced and withdrawn from the orbit border. The skull table of *Drinosaurus* is shorter than in the brachyopids. Watson "writes off" such features as a movable basal articulation and the greater anterior extent of the pterygoids in *Drinosaurus* as merely the retention of primitive characters. However, the retention of such a remarkably primitive feature as a movable basal articulation at such a late date is a condition one would hardly expect if we were, in *Drinosaurus*, confronted by an immediate brachyopid ancestor.

Other palatal structures of *Drinosaurus* are also features hardly to be expected in an immediate ancestor of the brachyopids. In *Drinosaurus*, the vomers are expanded to meet the pterygoids on the lateral border of the interpterygoid vacuities, so that the palatine, which in *Drinosaurus* is a remarkably small bone, takes no part in the border of the interpterygoid vacuity, whereas in brachyopids the palatine forms the anterior border of that opening. Perhaps significant is the presence of anterior palatal fenestrae in *Drinosaurus*— none are recorded in the brachyopids.

Some differences between *Drinosaurus* and the brachyopids may reflect a more primitive level of organization in *Drinosaurus* and its obvious neoteny. However, the number of morphological differences that exist between *Drinosaurus* and the brachyopids rule against a close relationship.

Eobrachyops is more like the brachyopids than is *Drinosaurus* in such features as: less broadly rounded snout; nares, though widely separated, closer together than in *Drinosaurus;* orbits of more "normal" proportions; very shallow cheek below orbit; pattern of postorbital region; lacrimal, though still in contact with orbit, greatly reduced; longer skull table than in *Drinosaurus;* entrance of palatine into the margin of interpterygoid vacuity.

On the other hand, such specialized characters in *Eobrachyops* as tiny tabulars, great reduction of sensory canal grooves, abbreviated maxilla, peculiar pattern of palatal bones adjacent to choanae, and position of quadrate articulation further forward than in some brachyopids, tend to remove it from a directly ancestral position.

In placing *Eobrachyops* close to the ancestry of the brachyopids, Watson listed five characters in which *Eobrachyops* and *Drinosaurus* resemble the brachyopids and "differ from all other labyrinthodonts" (1956, p. 365). This, which would appear to be a clinching argument, loses strength on closer examination. Two of the five characters, it is true, are found only in *Eobrachyops*, *Drinosaurus* and brachyopids. These are: (1) a distinct space, formerly occupied by a cartilaginous ridge on the posterior surface of the quadrate, separates the hinder border of the pterygoid from those of the squamosal and quadratojugal; (2) the outer surface of the squamosal and quadratojugal passes round onto the posterior face of the quadrate and there forms a laterally concave, nearly vertical surface.

However, the other three characters cited by Watson are not exclusive to *Eobrachyops*, *Drinosaurus* and the brachyopids, but are present in other trimerorhachoids (*Saurerpeton*, *Acroplous*), and two of the three — projecting occiput (metoposaurs, plagiosaurs) and ventral position of the quadrate condyle (edopsoids, eryopsoids) — may also be found in other labyrinthodont groups.

If *Eobrachyops* is a Permian representative of the brachyopids, special characters and typically advanced features in *Eobrachyops* would certainly debar *Drinosaurus* from a position intermediate between *Eobrachyops* and later brachyopids.

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PLATE 1

Neldasaurus wrightae, n. gen., n. sp. Holotype skull in dorsal view. MCZ 2200, Block A, × .66 approx.

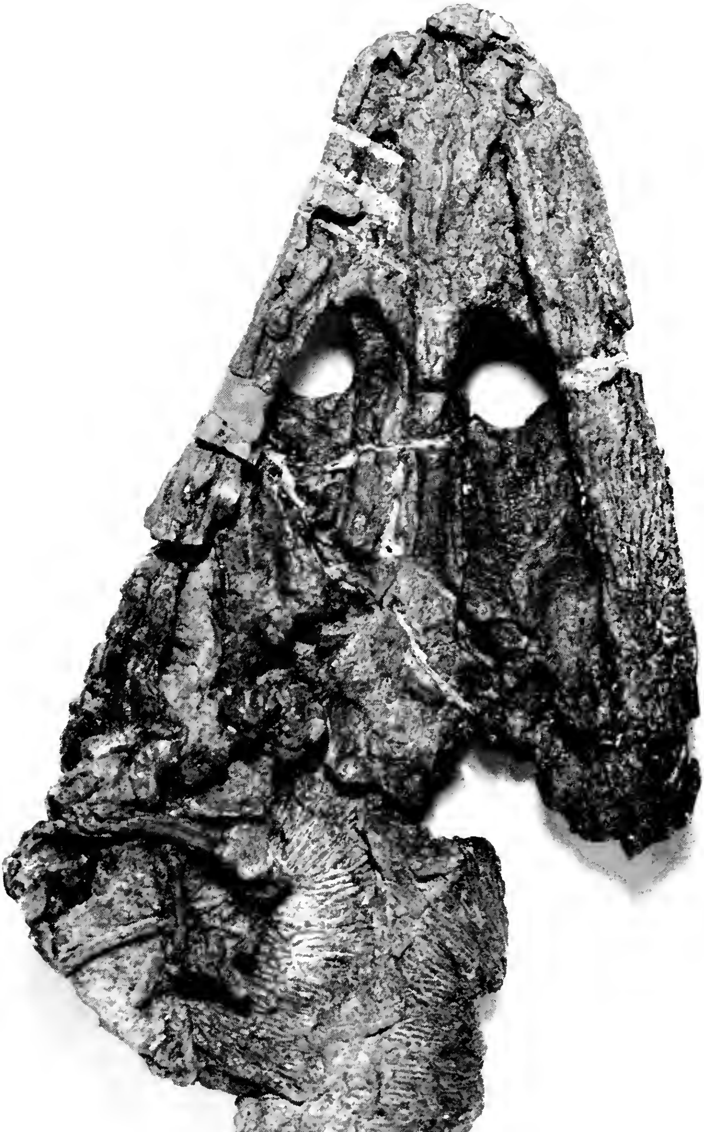

PLATE 2

Neldasaurus wrightae, n. gen., n. sp. Holotype skull in palatal view. MCZ 2200, Block A, × .66 approx.

PLATE 5

Neldasaurus wrightae, slab showing dorsal vertebrae in series and a partially articulated left forelimb. MCZ 1371. Block A, × 1 approx.

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By

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Museum of Comparative Zoology

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No. 4.—*The Genera of the Chilocorini (Coleoptera, Coccinellidae)*

By

Edward A. Chapin

INTRODUCTION

It is now ninety-one years since the latest attempt to evaluate the described genera of Coccinellidae of the world was made by G. R. Crotch (A Revision of the coleopterous family Coccinellidae, London, 311 pages, 1874). Since 1874, there has appeared a bibliographic catalog of the species of this family by R. Korschefsky (Coleopterorum Catalogus, Junk-Schenkling, Partes 118, 120, Coccinellidae, 659 pages, 1931-1932). A critical review of the genera and species of this family is long overdue but has now become virtually impossible for any one worker to accomplish. So it seems best to select some small, well circumscribed group within the family as a starting point. I have chosen the Chilocorini, a well known and easily recognized tribe.

This tribe is a very compact group of genera distributed generally throughout the world. In the Korchefsky catalog twenty-four generic or subgeneric names are listed. One of these, *Clanis*, is a preoccupied name that has already been replaced. A second, *Notolipernes*, had been placed as a synonym of *Telsimia* and removed from this tribe at the time that the catalog was going through press. *Corystes* Mulsant was described in the Hyperaspini, and its placement has been under discussion since Chapuis (*in* Lacordaire, 1876, Genera Coleopt., 12:244, 249) referred it to the Chilocorini. The genus is here returned to the Hyperaspini where it apparently belongs. I have found no explanation for the inclusion of *Elpis* Mulsant in the Chilocorini and, after an examination of the type species, *E. dolens* Mulsant, have returned it to the Coccinellini to a position near *Menochilus* Timberlake. There remain twenty names that are properly included in this tribe. Of these, I have been able to examine specimens, usually of the type species, of seventeen. In the course of my work I have found it necessary to propose two new genera. As far as possible the characterizations of the genera have been taken from the respective type species.

I wish to express my thanks to Dr. P. J. Darlington, Jr. for encouragement and assistance in securing necessary material for study, to Dr. R. D. Pope for specimens of *Elpis dolens* Mulsant, *Endochilus plagiatus* Sicard, and *Endochilus styx* Sicard, to Mr. E. B. Britton and Mr. G. F. Gross for specimens of three species of *Orcus*. My thanks are also due to Mrs. Morna MacLeod for preparing the illustrations from my tracings and to Mrs. Neil Barth for typing the manuscript.

Specimens for study have been dissected, the pertinent parts cleared of muscular tissue in cold KOH 10 per cent solution, and passed through the alcohols and oil of wintergreen (methyl salicylate) into Canada balsam. The drawings were made by tracing the outlines projected onto paper at various magnifications through a Bioscope projection apparatus. There follows a discussion of the parts studied.

STRUCTURE AND TERMINOLOGY

Antenna. The number of segments varies from ten to seven. The basal segment may be more or less cylindrical or it may be produced laterally at its apex in a rounded or subconical lobe (*Halmus, Priasus, Orcus*). The apical segment may be very short and embedded in the penultimate segment or it may be as long as or longer than the penultimate segment (*Anisorcus, Orcus, Chilocorus, Egius, Priasus*).

Mandibles. In place of the supplementary tooth (absent in all Chilocorini), there is a short knife-like ridge on the ventral aspect running backward a short distance from the apex. In general the mandibles follow a pattern throughout the Chilocorini. In three cases (*Axion, Egius, Priasus*) the apices are obtusely triangular, without the hooked tip of the others. In *Halmus*, the right, and to a lesser extent the left, mandible has a more or less broad triangular internal tooth. Rudiment of this tooth can be seen on the right mandible of *Anisorcus.*

Maxilla. I have not attempted to describe the differences which exist in the maxilla proper, but have confined my attention to the palpus. The terminal segment, described as securiform for the family as a whole, varies from that shape in several instances. In *Anisorcus, Egius,* and *Phaenochilus* the segment is cylindro-acuminate while in *Chilocorus* and *Priasus* the sides are almost parallel. In *Halmus* the segment is barrel-shaped with oblique apex.

Ligula. In general this sclerite is soft, quadrate, with anterior angles rounded. It bears the labial palpi which show some variation. The terminal segment may be shorter than the preceding, or longer, as in *Harpasus* and *Axion.* It may be slender, cylindro-acuminate as in *Exochomus* or short, stout, and conical as in *Halmus.*

The number of visible abdominal sternites has been considered as one of the prime characters in coccinellid taxonomy. However, in the Chilocorini, most of the genera have six visible sternites in the male and five in the female. This is because the fifth in the male is truncate or broadly emarginate, thereby disclosing the sixth sternite. In the genus *Orcus,* the fifth is as broadly rounded in the male as in the female, thereby concealing the sixth in both sexes. On the other hand, in the genera *Halmus, Anisorcus,* and *Egius,* the fifth is truncate or emarginate in the female as in the male, thereby disclosing the sixth in both sexes. Except for these slight differences, the fifth sternite is unmodified. The first visible sternite carries the metacoxal arcs — thin ridges arising at the sides of the intercoxal process of the sternite and extending out. In the Chilocorini we find the same types that have been long used in the classifications of the Scymnini. Thus, in *Exochomus, Brumus* (male), and *Brumoides* the arcs are complete or closed, as in *Pullus.* In *Axion, Brumus* (female), *Cladis* (*Clanis* renamed), *Curinus, Harpasus,* and *Zagreus,* the arcs are incomplete but directed forward at their extremities as in *Scymnus.* These genera are characterized by the presence of tibial spurs. The arcs are incomplete and directed outward at their extremities or are fused with the posterior margin of the sternite in those genera without tibial spurs. *Anisorcus, Orcus,* and *Priasus* have arcs directed outward, as in *Nephus,* while *Chilocorus, Egius,* and *Halmus* have arcs fused with the margin of the sternite as in *Diomus.*

Legs. The femora are unmodified throughout the group, except for a shallow groove for the reception of the tibiae. The tibiae show some modifications. In *Brumus* and *Brumoides,* the legs are unusually slender, and in *Brumoides* especially, the tibiae are many times longer than broad. Three genera, *Chilocorus, Egius,* and *Phaenochilus* have developed a stout, triangular tooth on the outer margin of the basal half of the tibia.

Claws. In general the form of the tarsal claws is characteristic of the genus. In this tribe there are three genera with completely simple claws (*Brumus*, *Brumoides*, and *Priasus*); claws with a very small triangular tooth basally or slightly postmedian are present in *Endochilus* and *Parapriasus* (in part); and claws with a heavy triangular or subquadrate tooth are in the other genera. Usually the type of claw can be determined from a dry specimen but it may be necessary to mount a claw in balsam in order to perceive a minute tooth as in *Endochilus* or in some species of *Parapriasus*. In the figures which accompany this paper, all illustrations of claws are drawn to the same scale.

Male genitalia. The *median lobe*, except in one genus, is triangular in dorsal view. It may be perceptibly asymmetrical as in *Axion*, *Chilocorus*, *Curinus*, *Egius* and *Exochomus*. It may be less than twice as long as broad, in *Brumoides* and *Cladis*, or as much as seven times longer than broad as in *Egius* and *Exochomus*. In *Egius*, the lobe is longer than the parameres, in other genera equal (*Chilocorus*) or shorter. The exception is the genus *Halmus*, in which case the lobe is parallel sided, longer than the parameres, the tip upturned and in side view concave in the basal two-thirds and again in the apical third. The *parameres* are slender throughout as in *Halmus* and *Priasus* or are moderately broad and spatulate and may be slightly or strongly constricted in basal half. In the genus *Anisorcus* they are very broad and concave, without any basal constriction. The *trabes* is simple, slightly curved, and slightly thickened at its free extremity. It is unusually thin in *Axion*. The *sipho* does not vary much from genus to genus. Moderately stout and curved, with the siphonal capsule more or less similar in all genera but *Anisorcus*, and the apex variously modified, the apex has more value for specific than for generic identifications. In the illustrations, the aedeagus and sipho are always drawn to the same scale.

Female genitalia. The *receptaculum seminis* is of a type not to be found, to the best of my knowledge, elsewhere in the Coccinellidae. The body is stout, very much so in the basal part, the ramus is entirely absent, the nodulus usually absent but represented in some genera (*Egius*, *Zagreus*) by a small button-like dome, and the cornu small, rounded, and bent at right angles to the body. In four genera (*Anisorcus*, *Chilocorus*, *Phaenochilus*, and *Egius*) most of the cornu is replaced by an appendix, definitely separate from the body. In the genus

Halmus the body is more slender and appears nearly coccinelline in its form. The *accessory gland* is moderate to very long, sometimes, as in *Axion*, several times as long as the receptaculum. The *sperm duct* is extraordinary as among Coccinellidae in my experience. The duct consists of two parts: one of small diameter arises at the head of the bursa copulatrix, at the base of the infundibulum, and connects with the second part of greater diameter, which leads to the receptaculum. These parts are roughly equal in length. Two genera deviate from the norm. In *Anisorcus*, the first part seems to be an extension of the bursa; it is of greater diameter than usual but is very thin-walled and definitely shorter than the second part. In *Halmus* the first part is longer than the second and almost as great in diameter. The *infundibulum* is present in all but four genera and is very variable in shape and size. In *Egius*, *Phaenochilus*, and *Chilocorus* it is replaced by a fleshy protuberance, unsclerotized, on the head of the bursa; in *Anisorcus* it is completely lacking. The *bursa copulatrix* in all genera is a simple thin-walled sac with no modifications, such as are seen in certain species of *Hippodamia*. The *hemisternites* (divided eighth sternite) are usually subtriangular, more or less elongate, each with a small button-like stylus at apex. In the genera *Endochilus*, *Anisorcus*, *Egius*, *Phaenochilus*, and *Chilocorus*, the styli are absent while in *Halmus* they are cylindrical and longer than wide.

In the key which follows it will be noticed that half of the genera studied lack tibial spurs, all but two of which (*Chilocorus* and *Egius*) are restricted to the Old World, while the other half of the genera possess tibial spurs and all but two (*Brumus* and *Brumoides*) are confined to the New World. Of these four exceptions, one of each pair is nearly worldwide, the other closely related to it. This suggests that *Brumoides* developed first in the New World, then spread into most of the Old World, with *Brumus* as an Old World offshoot, and that *Chilocorus* was originally an Old World genus which invaded the New World, with *Egius* as its New World segregate.

SYSTEMATIC SECTION

Tribe CHILOCORINI Costa

Costa, 1849, Fauna Regno Napoli, I:9.

Coccinellidae of small to large size, 2.0-8.0 mm, form oval to nearly circular, moderately to strongly convex, upper surface glabrous or pubescent. Antenna of less than eleven segments, short, terminal segments forming a fulsiform club, its origin concealed beneath the genal extension of the clypeus which enters or passes immediately beneath the eye. Mandible without supplementary apical or subapical tooth but with a sharp ridge which runs back a short distance from apex on the ventral face. Prosternal lobe without carinae. Abdomen usually with six visible sternites in male, five in female, sometimes five in both sexes or six in both sexes. Legs usually normal, occasionally with modified tibiae, tibiae with or without terminal spurs, tarsi four-segmented, tarsal claws simple, or swollen at base, or with basal tooth. Male genitalia: median lobe of aedeagus usually elongate triangular, compressed, often asymmetrical near apex, parameres shorter or longer than the median lobe, occasionally modified at apices. Female genitalia: receptaculum seminis very stout, somewhat bent, ramus absent, nodulus occasionally developed but never prominent, cornu a small terminal portion, sometimes with an appendix, accessory gland usually very large. Sperm duct very long, of two parts. The part leading into the receptaculum, usually half the total length, is a moderately coarse tube, the part leading from the bursa a thinner, usually much thinner, tube. Infundibulum present or absent; if present the sperm duct arises at its base. Bursa copulatrix a large, simple sac. Hemisternites usually elongate, sometimes short, subtriangular, rounded at apices, styli small, usually button-shaped with two to four long setae, sometimes absent.

KEY TO GENERA OF TRIBE

1\. Tibial spurs present on legs II and III, metacoxal arcs as in *Scymnus* or *Pullus*, antenna 10, 9, or 8-segmented 2

Tibial spurs absent on all legs, metacoxal arcs as in *Nephus* or *Diomus*, antenna 9, 8, or 7-segmented 9

2\. Tarsal claw simple, sometimes slightly thickened at base 3

Tarsal claw with tooth in basal half, which is sometimes quadrate, sometimes acute, often very small 4

3\. Antenna 10-segmented, Old World *Brumus* Mulsant

Antenna 8-segmented, world-wide *Brumoides* n. gen.

4\. Antenna 10-segmented 5

Antenna 9-segmented *Harpasus* Mulsant
Antenna 8-segmented *Zagreus* Mulsant
5. Elytral epipleura foveolate for reception of tips of femora 6
Elytral epipleura not foveolate 8
6. Elytra without reflexed margins, with marginal bead, size small to moderate, up to 6 mm 7
Elytral margins feebly but distinctly reflexed, with or without marginal bead, size very large, up to 8 mm *Axion* Mulsant
7. Size larger, up to 6 mm, elytra blue, parameres not appendiculate *Curinus* Mulsant
Size smaller, up to 3.75 mm, elytra black or bluish black, with red basal spot, parameres appendiculate *Arawana* Leng
8. Metacoxal arcs complete or virtually so *Exochomus* Redtenbacher
Metacoxal arcs widely incomplete *Cladis* Mulsant
9. Receptaculum seminis without apical appendix, infundibulum usually present (absent in *Endochilus*) 10
Receptaculum seminis with an apical appendix, infundibulum absent 14
10. Antenna 9-segmented 11
Antenna with less than 9 segments 12
11. Tarsal claw without basal tooth but somewhat swollen at base, elytral margin feebly reflexed in apical half *Priasus* Mulsant
Tarsal claw with sharp quadrate basal tooth, elytral margin strongly reflexed throughout *Parapriasus* n. gen.
12. Upper surface wholly or in large part pubescent, infundibulum absent *Endochilus* Weise
Upper surface glabrous, anterior angles of pronotum sometimes sparsely hairy, infundibulum present 13
13. Antenna 7-segmented *Halmus* Mulsant
Antenna 8-segmented *Orcus* Mulsant
14. Antenna 7-segmented, all tibiae without tooth on outer margin in basal half *Anisorcus* Crotch
Antenna 8-segmented, tibiae II and III, sometimes I, with triangular tooth on outer margin at extremity of tarsal groove 15
15. Terminal segment of maxillary palp one and one-half times as long as wide, its apex strongly oblique, elytral margin feebly reflexed *Chilocorus* Leach
Terminal segment of maxillary palp two or three times as long as wide, apex acuminate 16
16. Elytra strongly alutaceous, the lateral margins not reflexed, terminal segment of maxillary palp about twice as long as wide, cylindro-acuminate, tooth on tarsal claw weak, New World *Egius* Mulsant
Elytra not alutaceous, the lateral margins strongly reflexed, terminal segment of maxillary palp three times as long as wide, gradually narrowed to a blunt point, tooth on tarsal claw very strong, nearly as long as apical portion of claw, Old World *Phaenochilus* Weise

BRUMUS Mulsant

Brumus Mulsant, 1850, Species Trimères Sécuripalpes, p. 492; Crotch, 1874, Revision of the Coccinellidae, p. 195; Weise, 1885, Best.-Tab. Europ. Coleopt., Coccinelliden, II, ed. 2, p. 5.

Type species. Coccinella octosignata Gebler, through synonymy with *C. desertorum* Gebler, by subsequent designation of Crotch, 1874.

Chilocorini with form broadly oval, moderately convex, upper surface glabrous. Antenna ten-segmented; first segment stout, less than twice as long as wide, constricted at base; second almost as wide as first, slightly longer than wide; third to fifth mutually similar in form, the fifth shorter; sixth and seventh mutually similar, each wider than long; eighth and ninth large, eighth almost as long and ninth longer than sixth and seventh together; tenth small, more or less embedded in the oblique apex of the ninth. Mandibles stout, somewhat angulate on the outer margin. Terminal segment of maxillary palp rather elongate, apex strongly oblique, lacinia with a row of three shorter spines along the edge of the row of long setae. Terminal segment of labial palp cylindro-acuminate, rounded

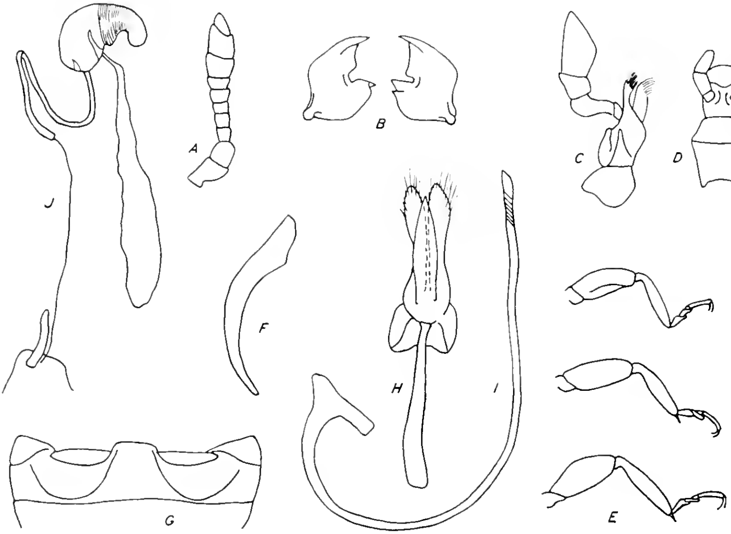

FIG. 1. *Brumus octosignatus* (Gebler). In this figure and all subsequent figures the lettering is as follows: *A* — antenna, *B* — mandibles, *C* — maxilla, *D* — ligula, *E* — legs, *F* — claw, *G* — first abdominal sternite, *H* — aedeagus, *I* — sipho, *J* — sclerotized portions of female genitalia.

at apex. Prosternal lobe moderately wide, truncate at apex. Elytra with lateral margins very slightly reflexed, finely beaded, epipleura not foveolate for reception of the femoral apices. Abdomen with six visible sternites in male, five in female. Metacoxal arcs almost complete in male, widely incomplete in female. Legs slender, femur of leg III a little stouter than the others, tibial spurs present, tarsal claws unusually long and slender, without basal tooth or swelling. Male genitalia: median lobe lanceolate, slightly wider at middle of length, four and one-half times as long as greatest width; parameres moderately wide at base and apex, constricted near middle of length, slightly longer than the median lobe; trabes rather stout, as long as the main parts of the aedeagus; sipho rather long and slender, of nearly uniform diameter through most of its length, apex blunt, with a series of oblique lines or grooves shortly before apex. Female genitalia: receptaculum seminis stout, cornu rather small, bent and rounded; accessory gland large; sperm duct shorter than usual, the parts equal in length, the slender part very slender; infundibulum present, rather longer than usual; hemisternites short and blunt, triangular, apices rounded, styli apical, button-shaped, with two or three long setae each.

This genus was established by Mulsant to include two species, *Coccinella desertorum* Gebler (=*C. octosignata* Gebler) and *Coccinella suturalis* Fabricius. I have removed the second species to serve as the type of a new genus, *Brumoides*. *Brumus octosignatus* (Gebler) is the only species of *Brumus* known to me.

BRUMOIDES new genus

Brumus,—Leng, 1908, Journ. New York Ent. Soc., 16:34; Casey, 1908, Can. Ent., 40:409.

Type species. *Coccinella suturalis* Fabricius, by present designation.

Chilocorini with form oval, moderately convex, upper surface glabrous. Antenna eight-segmented; first segment short and stout, slightly bent; second, as wide as first at base, gradually tapering to half that width at apex; third, fourth, and fifth similar and nearly equal, all slightly longer than wide; sixth one and one-half times longer than wide, of nearly the same diameter as fifth; seventh about equal in length to sixth, apex obliquely truncate; eighth small, partly embedded in apex of seventh. Mandibles not heavily developed, outer margin strongly convex in apical two-thirds, concave in basal third. Terminal segment of maxillary palp securiform with apex strongly oblique, lacinia with row of three short, stout spines along the edge of the row of longer setae. Labial palp rather long and slender, the terminal segment cylindro-acuminate, the apex rounded. Prosternal lobe narrow, truncate. Elytral margin very finely reflexed, with bead, epipleura not foveolate for the reception of the femoral apices. Abdomen with six visible sternites in male, five in female. Metacoxal arcs complete. Legs slender, femora not noticeably inflated, tibiae slender, tibial spurs present, tarsi rather long, tarsal claws moderately long, slightly thickened at base but without angular basal tooth. Male genitalia: median lobe triangular, less than twice as long as wide at base; parameres thin, spatula-shaped, hardly at all constricted in basal half, nearly twice as long as median lobe; trabes rather slender, equal in length to the main parts of the aedeagus; sipho moderately slender, of nearly even diameter in basal half, tapering slightly in apical half, apex twisted and terminating in a short finger-like process. Female genitalia: receptaculum seminis much as in *Brumus*; sperm duct moderately long, the thin portion not much more slender than the thick portion; infundibulum present, small; hemisternites moderately long, parallel-sided to just before apices where they taper to blunt points,

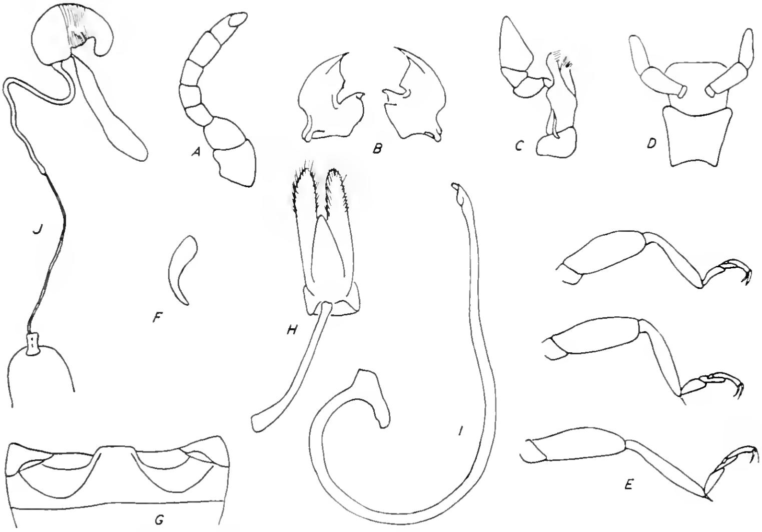

FIG. 2. *Brumoides suturalis* (Fabricius).

styli small, button-shaped, with two or three long setae from each.

The following species have been studied and belong to *Brumoides*: *Coccinella suturalis* Fabricius, *Exochomus foudrasii* Mulsant, *E. hoegei* Gorham, *E. desertorum* Casey, *E. parvicollis* Casey, *E. histrio* Fall, *Exochomus* (*Brumus*) *davisi* Leng, *E.* (*B.*) *nevadensis* Leng, *Brumus septentrionis* Weise.

HARPASUS Mulsant

Oreus (*Harpasus*) Mulsant, 1850, Species Trimères Sécuripalpes, p. 473.

Harpasus, — Crotch, 1874, Revision of the Coccinellidae, p. 190 (as synonym of *Curinus* Mulsant).

Type species. Orcus (*Harpasus*) *pallidilabris* Mulsant, by subsequent designation of Crotch 1874.

The ensuing description has been taken from specimens of *Orcus* (*Harpasus*) *zonatus* Mulsant, one of the originally included species.

Chilocorini with form very broadly oval, nearly circular, moderately convex, upper surface glabrous. Antenna nine-segmented; first segment short and stout, narrowed at base; second as long but not quite as wide as first; third about as long as width at apex which is twice width at base; fourth to sixth mutually similar in shape, the fourth half as long as third and slightly wider; fifth and sixth each a little longer and wider than the preceding segment; seventh almost as long as fifth and sixth combined and still wider; eighth more than twice as long as seventh, sides nearly parallel; ninth small, conical. Mandibles with outer margin feebly concave in basal half, then sharply convex to apex. Terminal segment of maxillary palp elongate, the sides nearly parallel, the apex strongly oblique, lacinia with row of four short, stout spines along the edge of the row of longer setae. Terminal segment of labial palp cylindro-acuminate, rounded at apex. Prosternal lobe rather broad, its lateral margins strongly grooved, the groove then following the margin of the coxal cavity. Elytral margin narrowly reflexed, finely beaded, epipleura foveolate for the reception of the femoral apices. Abdomen with six visible sternites in male, five in female. Metacoxal arcs widely incomplete. Legs slender, the femora not much enlarged, tibiae simple, tarsi normal, tarsal claws bent, basal tooth large, quadrate. Male genitalia: median lobe lanceolate, greatest width in basal third, four times as long as wide; parameres spoon-shaped, strongly

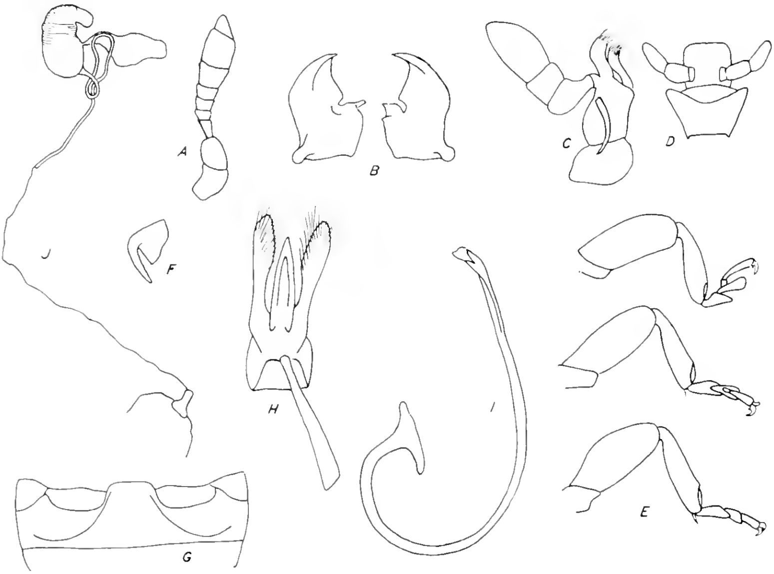

FIG. 3. *Harpasus zonatus* Mulsant.

constricted in basal half, longer than the median lobe by its greatest width; trabes rather stout, a little longer than the median lobe; sipho stout, of uniform diameter throughout most of its length, apex slightly twisted. Female genitalia: receptaculum seminis stout, cornu small; just before the cornu the body is girdled by a slightly prominent band; sperm duct long, the thick portion relatively not as thick as usual, the thin portion extremely thin; infundibulum present; hemisternites triangular, rounded at the apices, styli small, button-shaped, with two or three long setae each.

Harpasus zonatus Mulsant is the only species belonging to this genus that I have been able to study. From descriptions, it appears to be quite distinct from the type species, *H. pallidilabris* Mulsant and an examination of that species may show that the two are not congeneric.

ZAGREUS Mulsant

Exochomus (*Zagreus*) Mulsant, 1850, Species Trimères Sécuripalpes, p. 488.
Type species. Exochomus (*Zagreus*) *bimaculosus* Mulsant, by present designation.

Chilocorini with form very broadly oval to nearly circular, moderately convex, upper surface glabrous. Antenna eight-segmented; first segment stout, slightly bent, half again as long as wide; second as stout at base as first, tapering to apex, as long as wide; third and fourth nearly equal in length, each wider at apex than at base, fourth wider than third; fifth as long as fourth but wider; sixth as long as wide; seventh about as long as first, with apex strongly oblique; eighth short, conical, embedded in seventh. Mandible moderately stout, its outer margin broadly curved. Terminal segment of maxillary palp subsecuriform with apex strongly oblique, lacinia with oblique row of seven slender spines on outer face. Terminal segment of labial palp cylindro-acuminate, a little more than twice as long as wide, truncate at apex. Prosternal lobe narrow. Abdomen with six visible sternites in male (in a related species), five in female. Metacoxal arcs incomplete, ending about half way to base of segment, posterior margin of fifth sternite broadly rounded in female. Legs with tibial spurs, femora moderately stout, tibiae slender, shallowly excavate near apices, the margin of excavation

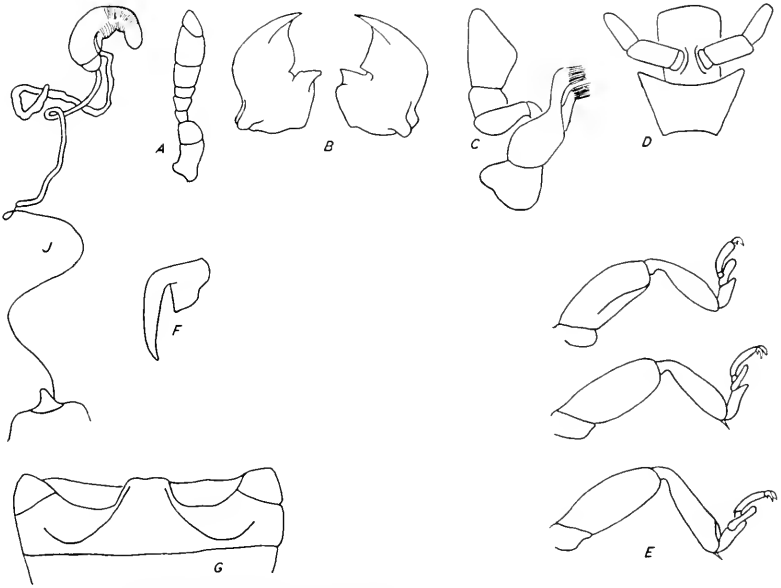

FIG. 4. *Zagreus bimaculosus* Mulsant.

edged with a row of slender bristles. Tarsal claws with stout, subquadrate basal tooth on each. Male genitalia not studied. Female genitalia: receptaculum seminis with nodulus distinct from body, but not prominent, cornu curved, rounded at apex, without appendix; accessory gland about twice as long as receptaculum; sperm duct long, the thick portion much thicker than the very thin portion; infundibulum present; hemisternites short and stout, triangular, about twice as long as wide at base, apices broadly rounded, styli short, button-shaped, with long setae.

The following species have been determined as belonging to the genus *Zagreus*. *Exochomus* (*Zagreus*) *bimaculosus* Mulsant, *E.* (*Z.*) *cinctipennis* Mulsant, *Exochomus jordani* Mulsant, *E. adelae* Crotch, *E. bistillatus* Weise, *E. decempunctatus* Weise, *E. guttatus* Weise, *E. subcoeruleus* Weise, and *E. ritchiei* Sicard.

Axion Mulsant

Exochomus (*Axion*) Mulsant, 1850, Species Trimères Sécuripalpes, p. 477.

Axion, — Crotch, 1874, Revison of the Coccinellidae, p. 191; Gorham, 1892, Biol. Centr.-Amer., Ins., Coleop., 7:176; Casey, 1899, Journ. New York Ent. Soc., 7:105; Leng, 1908, Journ. New York Ent. Soc., 16:34.

Type species. Coccinella tripustulata DeGeer, by subsequent designation of Crotch, 1874.

Chilocorini with form subcircular, size large to very large, strongly convex, upper surface glabrous. Antenna ten-segmented; first segment almost straight, twice as long as narrow median portion; second barrel-shaped, very little longer than wide; third through sixth similar in shape, narrow at base and widening from base to apex; third as long as wide, fourth and fifth each shorter than the preceding segment, sixth slightly longer than fifth; seventh through tenth forming a compact oval club, seventh and eighth equal in length, ninth longer with the apex oblique, tenth small, deeply embedded in ninth, conical. Mandible very stout, subangulate near middle of outer margin. Terminal segment of maxillary palp wider toward apex than at base, apex strongly oblique, lacinia with an irregular row of seven or eight stout spines on the outer side. Terminal segment of labial palp cylindro-acuminate, two and one-half times longer than wide. Prosternal lobe narrow, truncate at apex. Pronotum without fine marginal line across base. Elytra with lateral margins slightly reflexed, epipleura with very small foveae for reception of the femoral apices. Abdomen with six

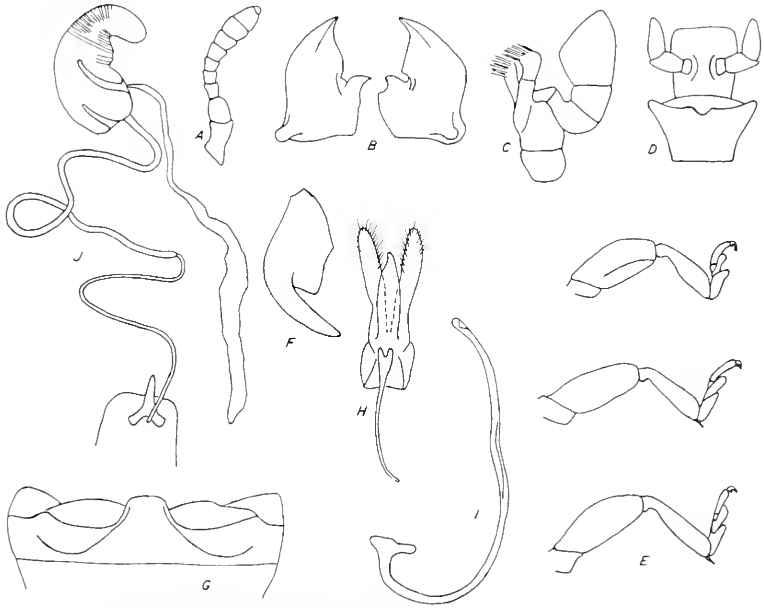

FIG. 5. *Axion tripustulatum* (DeGeer).

visible sternites in male, five in female, fifth sternite of male broadly emarginate. Metacoxal arcs broadly incomplete. Femora not noticeably stout, tibiae moderate, feebly excavated at apices for reception of first segments of tarsi, tarsal claw with very strong quadrate, plate-like tooth in basal half. Male genitalia: median lobe long, slender, slightly asymmetrical in apical third; parameres noticeably longer than median lobe, paddle-shaped and constricted at basal third; trabes very slender, about as long as a paramere; sipho slender, siphonal capsule well developed, apex of sipho blunt, slightly twisted. Female genitalia: receptaculum seminis much as in *Curinus;* sperm duct proportionately shorter than in *Curinus* and differing in that the thick portion is longer than the thin portion; infundibulum present, inverted Y-shaped; hemisternites parallel nearly to apices, then rounded triangular, styli button-shaped, each with three or four long setae.

This purely North American genus is in need of revision. Eight trivial names have been associated with the generic name *Axion;* four of these were considered as valid specific names in the world catalog.

CURINUS Mulsant

Orcus (*Curinus*) Mulsant, 1850, Species Trimères Sécuripalpes, p. 472.
Curinus, — Crotch, 1874, Revision of the Coccinellidae, p. 190; Gorham, 1892, Biol. Centr.-Amer., Ins., Coleop., 7:176; Korschefsky, 1932, Coleopt. Catalogus (Junk), pars 120, p. 252.
Type species. *Orcus* (*Curinus*) *coeruleus* Mulsant, monobasic.

Chilocorini with form nearly circular, strongly convex, upper surface glabrous. Antenna ten-segmented; first segment stout, slightly curved, slightly longer than wide; second barrel-shaped, one and one-half times longer than wide and nearly as wide as the first; third half as wide at base as second, nearly twice as wide at apex as at base: fourth nearly equilateral but slightly wider apically; fifth through tenth forming a compact fusiform club; fifth slightly wider than long; sixth and seventh almost equal in length, each wider at apex than at base; eighth longer and wider than seventh, maximum width of club at apex of eighth: ninth about twice as long as eighth, sides gradually tapering to apex which is oblique: tenth short and conical,

FIG. 6. *Curinus coeruleus* Mulsant.

slightly wider than long. Mandible stout, subangulate at middle of outer margin. Terminal segment of maxillary palp with lateral margins subparallel and apical margin strongly oblique, lacinia with irregular row of five stout spines on outer face. Terminal segment of labial palp elongate cylindrical but with outer margin slightly curved, about three times longer than wide. Prosternal lobe flat, moderately broad. Elytral margins slightly reflexed, with fine marginal bead, epipleura foveolate for the reception of the femoral apices. Abdomen with six visible sternites in male, five in female, apical sternite of male emarginate or notched, of female simple and rounded. Metacoxal arcs on first sternite incomplete, failing to reach base of sternite. Legs with femora moderately stout, tibiae near apices shallowly excavate, the margins of the excavation edged with rows of slender bristles, tarsal claws stout with subquadrate basal tooth. Male genitalia: median lobe slightly asymmetrical; parameres longer than the median lobe, constricted near basal third; trabes slender, about as long as paramere; sipho moderately stout, of even diameter nearly to apex, where the tube undergoes a quarter turn, the apex truncate. Female genitalia: receptaculum seminis more or less globular, basal portion without well-defined nodulus or ramus, cornu short, small, and bent; accessory gland long and slender; sperm duct very long, the thin part about twice as long as the thick part; infundibulum present, inverted Y-shaped; hemisternites elongate triangular, styli button-shaped, with three or four long setae from each.

With the removal of *Curinus peleus* (Mulsant) to *Exochomus*, and the reestablishment of *Harpasus*, with the transfer of its species from *Curinus* to it, *Curinus* is left with the type species and one very doubtfully included species from Chile, *Curinus ruizi* Brèthes. Brèthes figures the antenna as having eleven segments, which if true, makes that species unique in the tribe. I think it more likely that there is an error in the drawing and that the species belongs in *Harpasus*.

ARAWANA Leng

Exochomus (Arawana) Leng, 1908, Journ. New York Ent. Soc., 16:34, 38; Casey, 1908, Can. Ent., 40:409.

Type species. Exochomus arizonicus Casey, by original designation of Leng.

Chilocorini with form broadly oval, strongly convex, upper surface glabrous. Antenna ten-segmented; first segment short and stout, bent at almost a right angle; second equally stout, as long as wide; third strongly wedge-shaped, much narrower at base than at apex, about as long as width at apex; fourth to seventh similar in shape; fourth and fifth nearly equal, sixth and seventh each slightly wider and longer than the preceding segment; eighth one-half longer but hardly wider than seventh, ninth twice as long as eighth and as wide, its apex strongly oblique; tenth small, embedded in apex of ninth. Mandibles stout, somewhat angulate at middle of outer margin. Terminal segment of maxillary palp twice as long as wide, apex strongly oblique, lacinia with irregular row of six stout spines along the edge of a row of long setae. Terminal segment of labial palp slender cylindro-acuminate, rounded at apex. Prosternal lobe moderately broad, truncate. Elytral margin not reflexed, very finely beaded, epipleura foveolate for the reception of the femoral apices. Abdomen with five visible sternites in both sexes. Metacoxal arcs nearly complete. Legs moderately stout, femur of leg I a little stouter than the others, tibia I with the outer margin expanded into a thin keel, tibiae II and III with spurs, tarsal claws stout, strongly hooked, with triangular tooth in basal half. Male genitalia: median lobe lanceolate, four times longer than its greatest width at basal third; parameres noticeably longer than median lobe, strongly constricted near

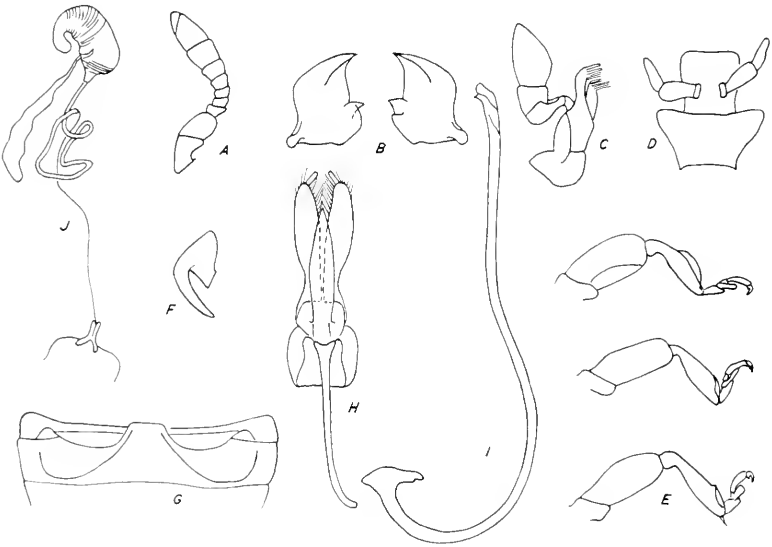

Fig. 7. *Arawana arizonica* (Casey).

base, each with a finger-like process at its apex; trabes slender, one and one-half times as long as the median lobe; sipho long in proportion to the aedeagus, of uniform diameter throughout most of its length, siphonal capsule small, apical portion of sipho slightly expanded and twisted. Female genitalia: receptaculum seminis much as in the genus *Curinus;* sperm duct with the thicker portion considerably longer than the extremely thin portion; infundibulum present, inverted Y-shaped; hemisternites about twice as long as wide, generally tapering to the blunt apices, styli apical, button-shaped, each with two or three long setae.

In addition to the type species, I am including two other species in the genus *Arawana, Exochomus scapularis* Gorham from Central America and *Exochomus cubensis* Dimmock from Cuba, this last with some hesitation. *E. cubensis* is included because, while the fore tibiae do not have the thin keel but are simply broadly curved on their outer margin, the male genitalia are quite similar to those of the other two species and do have the finger-like processes at the apices of the parameres. I consider the structure of the genitalia of more importance than that of the fore tibiae. All three species are similar in general appearance.

EXOCHOMUS Redtenbacher

Exochomus Redtenbacher, 1843, Tentamen dispositionis Coleopterorum pseudotrimerorum, p. 11; Reprint of above in Germar, 1844, Zeitsch. f. Ent., 5:121; Mulsant, 1850, Species Trimères Sécuripalpes, p. 476; Crotch, 1873, Trans. Amer. Ent. Soc., 4:376; 1874, Revision of the Coccinellidae, p. 192; Barovsky, 1922, Ann. Mus. Zool. Russie, 23:293, figs. 1a, 1b, 1c; Korschefsky, 1932, Coleopt. Catalogus (Junk), Coccinellidae, Pars 120, p. 252.

In 1922, Barovsky proposed a division of *Exochomus* into three subgenera, based on the structure of the tarsal claws, as follows:

I. Unguiculi dente *valido basali* instructi ....Subg. *Exochomus*, s.str.
II. Unguiculi dente *indistincto basali* instructi ....Subg. *Parexochomus* new
III. Unguiculi dente subacutangulo *post medium* instructi .. ..Subg. *Anexochomus* new

EXOCHOMUS (EXOCHOMUS) Redtenbacher

Exochomus (*Exochomus*) — Barovsky, 1922, Ann. Mus. Zool. Russie, 23:291, fig. 1a.

Type species. Coccinella 4-pustulata Linné (*quadripustulata* auct.), subsequent designation of Korschefsky, 1932. Two previous type designations for this genus had been made, both by Crotch and both invalid, since the species designated were not among those originally included.

Chilocorini with form broadly oval to almost circular, moderately convex, upper surface glabrous or pubescent. Antenna ten-segmented; first segment slightly curved, a little less than twice as long as wide; second barrel-shaped, as long as wide and same diameter as first; third obconical, half as long and half as wide as second; fourth, fifth, and sixth nearly equal, each slightly wider apically than at base; seventh similar in shape to sixth but about half as long as wide, and forming with the eighth, ninth, and tenth a slender fusiform club; eighth almost as long as wide, at base equal in width to apex of seventh, greatest width of club at apex of eighth; ninth as long as eighth, conical with apex strongly oblique; tenth small, conical deeply embedded in ninth. Mandible heavy, angulate at middle of outer face. Terminal segment of maxillary palp subsecuriform with apex strongly oblique, lacinia with row of five long, slender (not short, stout) spines on outer face. Terminal segment of labial palp cylindrical, twice as long as wide. Prosternal lobe narrow, truncate at apex, the anterior coxae almost contiguous. Pronotum very finely margined across base, lateral margins slightly reflexed. Elytral margin strongly beaded, epipleura not foveolate for the reception of the femoral apices. Abdomen with six visible sternites in male, five in female. Metacoxal arcs complete or virtually so. Legs with moderately stout femora, tibiae slender, tarsal claws strong, with subquadrate basal tooth on each. Male genitalia: median lobe long, slender, parallel in basal two-thirds, slightly asymmetrical in apical third; parameres about one-eighth longer than the median lobe, slender, somewhat constricted in basal half, spoon-shaped in apical half; trabes slender, almost as long as main body of the aedeagus; sipho moderately slender, of even diameter throughout most of its length, siphonal capsule rather heavy, apex of sipho twisted. Female genitalia: receptaculum seminis a stout body without clearly defined nodulus or ramus, cornu more slender than body, strongly curved; accessory gland slightly longer than receptaculum; sperm duct long, the parts about

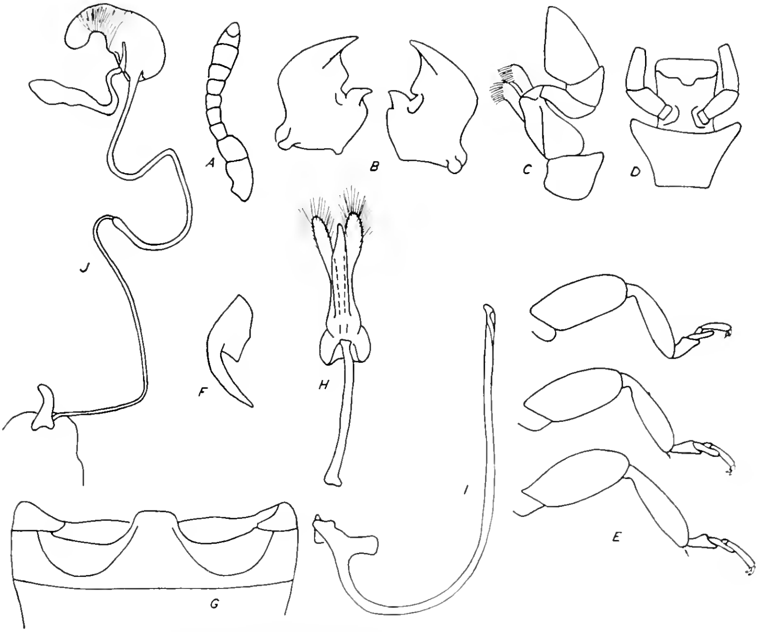

FIG. 8. *Exochomus quadripustulatus* (Linné).

equal in length, the thick part noticeably thicker than the thin part; infundibulum present, tapering slightly from a broad base and slightly curved; hemisternites elongate, subparallel, about three times as long as wide at base, apices acutely rounded, styli button-shaped, each with two or three long setae.

The following species have been verified as belonging to *Exochomus sensu stricto: Coccinella quadripustulata* Linné, *C. aethiops* Bland, *C. flavipes* Thunberg, *C. marginipennis* Leconte, *C. nigripennis* Erichson, *Orcus peleus* Mulsant, *Exochomus childreni* Mulsant, *E. californicus* Casey, *E. contristatus* Mulsant, *E. jamaicensis* Sicard, *E. latiusculus* Casey, *E. lituratus* Gorham, *E. metallicus* Korchefsky, *E. mormonicus* Casey, and *E. uropygidialis* Mulsant.

Eighteen species, originally described in *Exochomus,* have been removed from this genus. Two are here placed in *Arawana,* seven in *Zagreus,* and seven in *Brumoides.* Two species, *Exochomus tricoloratus* Gorham and *E. championi* Gorham are removed from the Chilocorini and should be placed in the Coccinellini near *Cycloneda.*

EXOCHOMUS (PAREXOCHOMUS) Barovsky

Exochomus (*Parexochomus*) Barovsky, 1922, Ann. Mus. Zool. Russie, 23:292, fig. 1b.

Type species. Exochomus pubescens Küster, by present designation.

I have been unable to examine any specimens conforming to Barovsky's description. Barovsky assigns the following palaearctic species to this subgenus: *E.* (*P.*) *pubescens* Küster, *E.* (*P.*) *anchorifer* Allard, *E.* (*P.*) *semenovi* Weise, and *E.* (*P.*) *kirgizorum* Barovsky.

EXOCHOMUS (ANEXOCHOMUS) Barovsky

Exochomus (*Anexochomus*) Barovsky, 1922, Ann. Mus. Zool. Russie, 23:292, fig. 1c.

Type species. Exochomus undulatus Weise, by present designation.

A single female specimen from Pusan, Korea, in the collection of the Museum of Comparative Zoology appears to be a color variant of *E.* (*A.*) *mongol* Barovsky. It satisfies the original description in every respect except that the subapieal spot on the elytron is missing. Its tarsal claws conform to figure 1c of the original description. A study of the gross anatomy shows no character of importance that would warrant a change of status for *Anexochomus.* Barovsky assigns the following species to this subgenus : *E.* (*A.*) *undulatus* Weise, *E.* (*A.*) *kiritshenkoi* Barovsky, and *E.* (*A.*) *mongol* Barovsky, all from the palaearctic region.

CLADIS Mulsant

Exochomus (*Clanis*) Mulsant, 1850, Species Trimères Sécuripalpes, p. 479 (name preoccupied).

Exochomus (*Cladis*) Mulsant, 1850, *idem*, Appendix, p. 1033 (new name for *Clanis* Mulsant not Hübner 1819).

Cladis, — Crotch, 1874, Revision of the Coccinellidae, p. 192; Weise, 1883, Wien. Ent. Zeitsch., 2:67; Gorham, 1894, Biol. Centr.-Amer., Ins., Coleopt., 7:179.

Type species. Coccinella nitidula Fabricius, through synonymy with *Exochomus* (*Clanis*) *uva* Mulsant, by subsequent designation of Crotch, 1874.

Chilocorini with form broadly oval, moderately convex, upper surface glabrous. Antenna ten-segmented; first segment slightly bent, about one and one-half times longer than wide; second equal in width to first, almost equilateral; third as long as second but only half as wide; fourth nearly as wide as third, equilateral; fifth to eighth rather similar, each wider and shorter than the preceding; ninth large, equal to the seventh and eighth combined; tenth small, more or less embedded in the oblique apex of the ninth. Mandible with the outer margin moderately curved, with no unusual modifications. Terminal segment of maxillary palp broad and short, apex strongly oblique, lacinia with two or three stout spines along the edge of the row of long setae. Terminal segment of labial palp cylindro-acuminate, rounded at apex. Prosternal lobe narrow, truncate at apex. Elytra with lateral margin not reflexed, epipleura not foveolate for reception of the femoral apices. Abdomen with six visible sternites in male, five in female. Metacoxal arcs widely incomplete. Legs with femora not unusually stout, tibiae simple, rather slender, shallowly excavate near apices, tarsal claws strongly curved, each with a large, quadrate basal tooth. Male genitalia : median lobe acutely triangular, two and one-half times longer than wide at base; parameres very

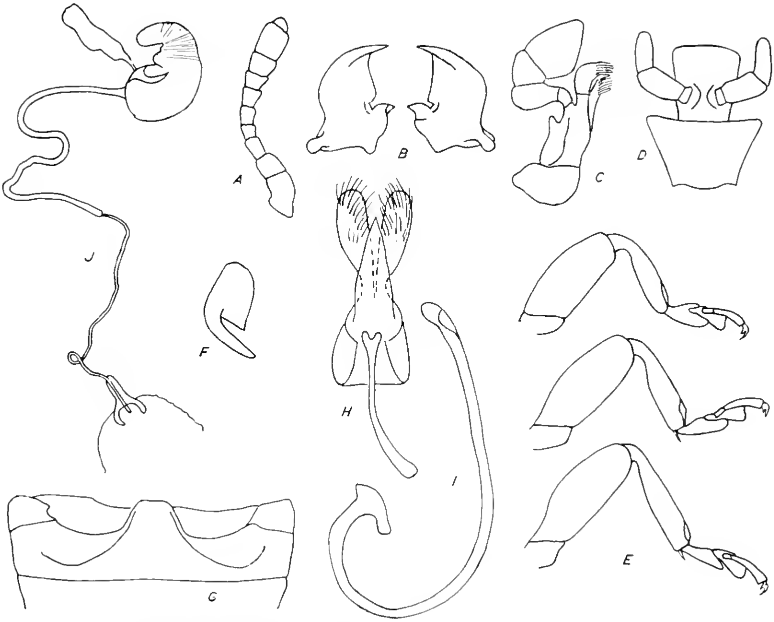

FIG. 9. *Cladis nitidula* (Fabricius).

broad in apical half, strongly constricted in basal half, noticeably longer than the median lobe; trabes moderately stout, curved, about as long as a paramere from basal attachment to apex; sipho moderately stout, of nearly uniform diameter throughout, apex somewhat twisted, blunt. Female genitalia : receptaculum seminis much as in *Curinus* or *Exochomus*, accessory gland moderate in size; sperm duct moderately long, the thick portion slightly longer than the thin portion; infundibulum present, inverted Y-shaped; hemisternites moderately heavy, elongate triangular, apices rounded, styli minute, button-shaped, each with two or three long setae.

Mulsant segregated two supposedly new species under the name *Clanis*, which name had been previously used by Hübner. At present it is considered that Mulsant's "species" are not distinct and are synonyms of the much earlier Fabrician species, which occurs on various of the West Indian islands. It has also been reported from Buenos Aires.

PRIASUS Mulsant

Orcus (*Priasus*) Mulsant, 1850, Species Trimères Sécuripalpes, p. 467; Crotch, 1874, Revision of the Coccinellidae, p. 188.

Type species. Coccinella bilunulata Boisduval, by subsequent designation of Crotch, 1874.

Chilocorini with form nearly circular, strongly convex, upper surface glabrous. Antenna nine-segmented; first segment slightly bent, strongly constricted at middle, apically produced laterally in a small, rounded lobe; second stout, barrel-shaped, nearly equilateral; third, fourth, and fifth trapezoidal, decreasing in length and slightly increasing in width at apices; sixth longer than fifth and slightly wider; seventh and eighth each longer than the preceding, the eighth slightly produced laterally at apex; ninth longer than eighth, subcylindrical, apex slightly oblique. Mandible stout, the outer margin not strongly curved, apex unusually blunt. Terminal segment of maxillary palp with outer margin convex, inner margin concave, the sides nearly parallel, apex oblique; lacinia with regular row of four stout spines on outer face. Terminal segment of labial palp cylindro-acuminate, truncate at apex. Prosternal lobe rather narrow, slightly dilated behind, apex rounded. Pronotum with a strong marginal line. Elytra with lateral margins only slightly reflexed, epipleura not foveolate for the reception of the femoral apices. Abdomen with six visible sternites in male, five in female; metacoxal arcs incomplete, running almost into the posterior margin of the sternite in female, curving toward anterior margin for a short distance in male. Legs stout, anterior femora about twice as long as wide, tibiae simple, slightly expanded apically, tarsal claws short and stout, swollen at base, without basal tooth. Male genitalia: median lobe elongate triangular; parameres straight, parallel-sided, rounded at apices, noticeably longer than median lobe; trabes as long as a paramere with its basal attachment; sipho slender, of even diameter except near the siphonal capsule where it is somewhat thicker, apex twisted and with a short, sharp apical process.

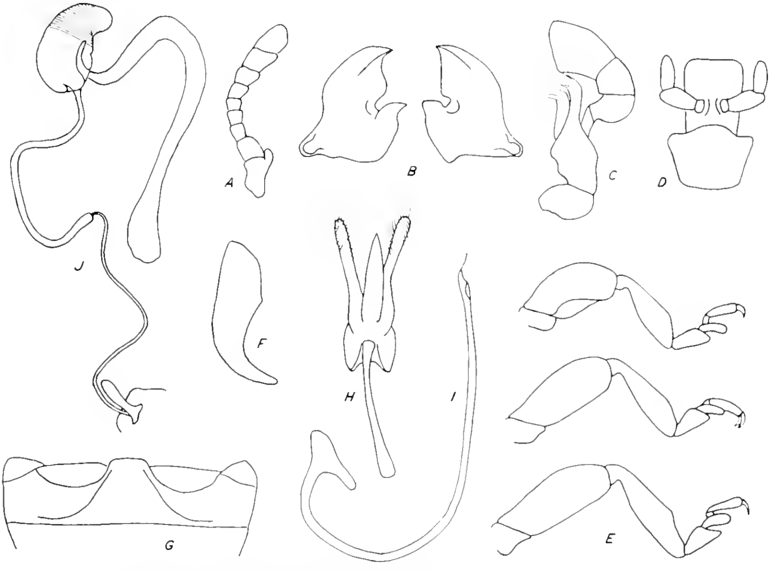

FIG. 10. *Priasus bilunulatus* (Boisduval).

Female genitalia : receptaculum seminis stout bulbous, nodulus hardly differentiated, ramus absent, cornu short, stout, and rounded; accessory gland about four times longer than the receptaculum; sperm duct rather short, the thick portion equal in length to the thin portion and about three-fourths as long as the accessory gland; infundibulum present; hemisternites elongate, the sides almost parallel to near apices which are abruptly narrowed and rounded, styli button-shaped, hardly prominent, each with two or three long setae.

Mulsant placed three species, all Australian, under this name. I have been able to study all three and have found that, while the type species has toothless claws, the other two have claws which are equipped with a basal tooth on each. In one case, *Coccinella australasiae* Boisduval, the tooth is large and conspicuous, in the other, *C. nummularis* Boisduval, the tooth is much smaller and is somewhat transparent and difficult to see. These two species have been referred to the following genus.

PARAPRIASUS new genus

Type species. Coccinella australasiae Boisduval, by present designation.

Chilocorini with form nearly circular, strongly convex, upper surface glabrous. Antenna nine-segmented; first segment a little longer than second, bent, constricted at basal third, apically widened; second barrel-shaped, wider at base than at apex, nearly equilateral; third to seventh similar in shape, third longer than wide, fourth shorter than third, fifth shorter than fourth or sixth, seventh as long as sixth but slightly wider; eighth longer than wide; ninth longer than eighth and tapering to a blunt point. Mandible stout, apex short and acute, outer margin subangulate at middle of length. Terminal segment of maxillary palp subsecuriform, apex oblique; lacinia with a patch of three or four short and stout bristles, in addition to the row of long setae. Terminal segment of labial palp cylindro-acuminate, rounded at apex. Prosternal lobe moderate, convex, margined laterally, the bead prolonged part way around the coxal cavity. Elytral margin rather strongly reflexed, without marginal bead; epipleura not foveolate for the reception of the femoral apices. Abdomen with six visible sternites in male, five in female, the fifth sternite broadly truncate in male, broadly rounded in female. Metacoxal arcs broadly open, the line running from the intercoxal process out and back almost to the posterior margin of the sternite, then curving forward for a short distance. Legs moderately stout, tibiae slightly widened toward apices, tibia I with a row of small denticles along outer margin, tarsal claw stout, with a subquadrate, translucent tooth in basal half. Male genitalia: median lobe about as long as the parameres, slender, elongate triangular but with the lateral margins nearly parallel in basal two-thirds, apical third tapering to a slender blunt apex; parameres slender, not noticeably constricted, apices broadly rounded; trabes slender, slightly curved, a little shorter than the median lobe; sipho

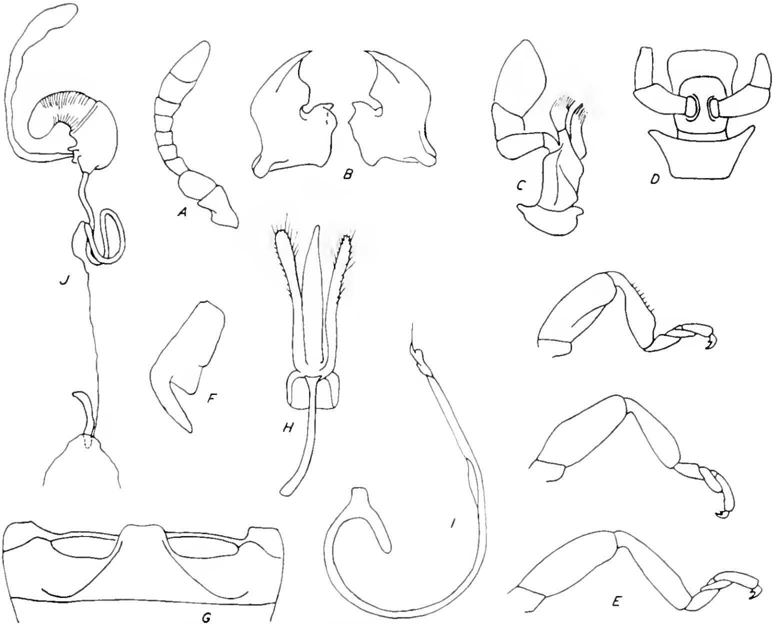

FIG. 11. *Parapriasus australasiae* (Boisduval).

rather similar to that of *Priasus*. Female genitalia : receptaculum seminis similar in shape to that of *Priasus* but less stout, especially the cornu; accessory gland about twice as long as receptaculum; sperm duct with thick portion a little longer than the very thin portion; infundibulum a simple, bar-like structure; hemisternites long, slender, and tapering to blunt apices, styli terminal, button shaped, each giving rise to two or three long setae.

Two species have been seen which belong to this genus, *Coccinella australasiae* Boisduval and *C. nummularis* Boisduval, both from Australia. In the latter the tooth on the tarsal claw is less well developed and less easily seen.

ENDOCHILUS Weise

Endochilus Weise, 1898, Deutsch. Ent. Zeitsch., p. 119, pl. 1, fig. 10, 1910, Verh. Naturf. Ver. Brünn, 48:52; Sicard, 1929, Ann. Mag. Nat. Hist., (10) 4:518.

Type species. Endochilus cavifrons Weise, by subsequent designation of Korschefsky, 1932.

As the type species is not available to me, I have prepared the generic description and illustrations from specimens of *E. plagiatus* Sicard.

Chiloeorini with form nearly circular, not strongly convex, margins broadly but not abruptly reflexed, upper surface wholly or partly set with fine pubescence. Antenna eight-segmented; first segment constricted at middle, twice as long as width at constriction; second elongate globose, slightly shorter and wider than first; third, fourth, and fifth wedge-shaped, each slightly shorter and wider than the preceding, third and fourth together about as long as the second; sixth longer and wider than fourth and fifth together; seventh slightly longer than sixth but hardly wider, the margins nearly parallel; eighth conical, as long as sixth, its apex rounded. Mandible with outer margin evenly curved. Maxillary palp very stout, the terminal segment elongate-conical, four times as long as the penultimate segment; lacinia with a row of four short, stout spines on outer face. Labial palp stout, the terminal segment conical, a little longer than the penultimate segment. Prosternal lobe broad, flat, not margined. Elytral margin subexplanate, slightly reflexed, without bead; epipleura weakly foveolate for the reception of the femoral apices. Abdomen with five visible sternites in either sex, in both the fifth sternite is broadly rounded. Metacoxal arcs run from the sides of the rather broad intercoxal process almost straight toward the posterior angles of the sternite, where the lines are slightly recurved. Legs slender, femur I a little stouter than the others, tibiae simple, tarsal claws gently and evenly curved, each with a small, obtuse, triangular tooth at base. Male genitalia: median lobe lanceolate, its greatest width at middle of length, apex acuminate; parameres slightly longer than the median lobe, their bases concave and partly embracing the lobe; trabes slender, about as long as median lobe, gradually broadened from apical third to apex; sipho long and slender, of nearly uniform diameter throughout most of its length, siphonal capsule small, apical portion slightly enlarged just back of the acuminate apex. Female genitalia: receptaculum seminis bent sausage-shaped, strongly constricted at basal fourth, nodulus not prominent, cornu stout, without apical appendix, accessory gland small, globular; sperm duct short, the thick portion shorter than the length of the receptaculum, the thin portion

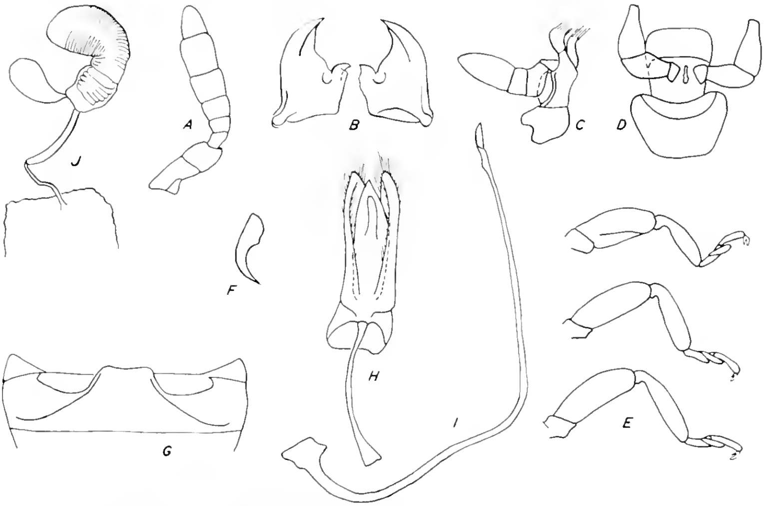

FIG. 12. *Endochilus plagiatus* Sicard.

shorter than the thick portion; infundibulum absent; hemisternites elongate, sides nearly parallel, about five times longer than average width, apices rounded, styli absent, represented by two long, apically placed, setae.

A genus of a few, below average size, species, mostly from West Africa south of the Gulf of Guinea. The genus is immediately distinguished from other chilocorine genera by the peculiar conformation of the head. The genal lobes and the clypeus form the transverse frontal margin of the head, with a forward extension below the eyes equal to half the long diameter of the eye. This margin passes below the eye and joins the temporal areas of the head. Thus there is no invasion of the eye itself.

HALMUS Mulsant

Orcus (*Halmus*) Mulsant, 1850, Species Trimères Sécuripalpes, p. 471.
Halmus, — Weise, 1923, Arkiv Zool., 15(12):134.
Type species. Coccinella chalybea Boisduval, the genus being originally monobasic.

Chilocorini with form nearly circular, moderately convex, upper surface glabrous. Antenna seven-segmented; first segment bent, constricted in basal half, apically produced laterally in a conical lobe; second nearly equilateral, barrel-shaped; third slender, twice as long as wide, the apex oblique; fourth and fifth similar in shape and proportions, the fifth half again as large as the fourth; sixth as wide at base as fifth, beyond middle it tapers to half its basal diameter; seventh conical, slightly longer than its diameter at base. Mandibles rather delicate, the outer margins strongly curved, apices acute; just distad of the median notch the inner margin is cut away so that it appears to be tridentate. Terminal segment of maxillary palp broadly oval, the apical margin oblique; lacinia with an irregular row of six or seven stout spines on outer face. Terminal segment of labial palp short, stout, and conical. Prosternal lobe moderately broad, truncate at apex. Pronotum without basal marginal line. Elytra with lateral margins reflexed, epipleura not foveolate for the reception of the femoral apices. Abdomen similar in both sexes, with six visible sternites, the fifth sternite in both sexes truncate. Metacoxal arcs incomplete, running parallel and close to the posterior margin of the sternite. Legs with femora not noticeably stout, tibiae simple, tarsal claws strongly curved, with broad, quadrate, plate-like tooth in basal half. Male genitalia: median lobe long, narrow, parallel-sided nearly to apex where it is rounded, as seen in dorsoventral view; in

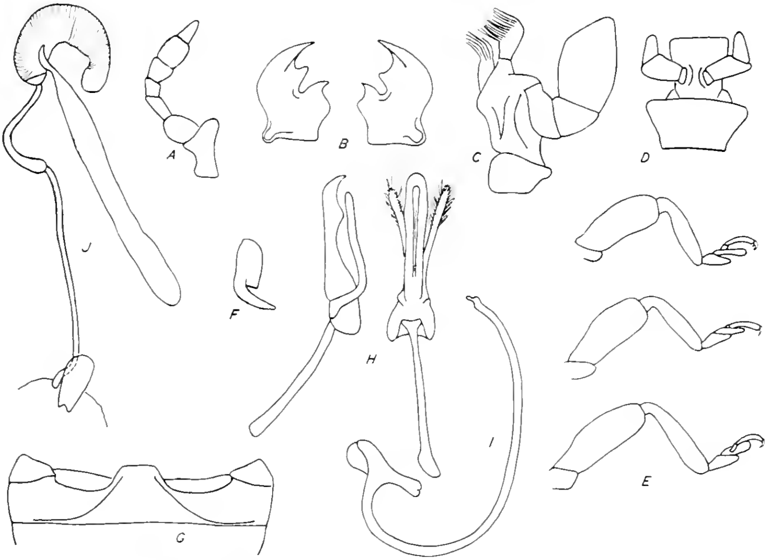

FIG. 13. *Halmus chalybeus* (Boisduval).

lateral view it is somewhat slipper-shaped, the apex or "toe" turned up and with a triangular projection in the dorsal margin at apical third; parameres very slender, slightly shorter than the median lobe; trabes a little longer than body of aedeagus; sipho slender, of even diameter throughout, apex somewhat twisted and with a short process. Female genitalia : receptaculum seminis curved, sausage-shaped, nodulus and ramus not defined, cornu separated from the main body by a slight constriction and broadly rounded apically, accessory gland longer than the receptaculum; sperm duct comparatively short, the thick section shorter than the thin section but of almost the same diameter except at the junction point; infundibulum present; hemisternites short, and broadly triangular, styli cylindrical, nearly twice as long as the diameter at base, each with two long setae.

Halmus chalybeus is a median sized species, 3.0-3.7 mm long, clear blue to blackish-blue above except that in the male the head and flanks of the pronotum are yellowish-white. This is one of the few genera that shows a sexual difference in coloration. The species is further distinguished by the unusual form of the genitalia of both sexes.

Weise was apparently the first to raise Mulsant's subgenus *Halmus* to full generic status. He did this because of the unusual shape of the genae. Here the genal lobe, which extends out over the antennal insertion and on into the eye, is abruptly narrowed at the inner margin of the eye and is continued into the eye as a fine line. This character, apparently unique among the Chilocorini, when taken together with the other characteristics which deviate from the norm, indicates that the genus stands in a rather isolated position in the tribe.

For the present, I am referring *Orcus ovalis* Blackburn to this genus. It agrees with *Halmus chalybeus* in its antennae, mandibles, ligula with labial palps, legs, metacoxal arcs, visible sixth sternite in the female, and receptaculum seminis. It differs in the broadly securiform maxillary palps, the male genitalia (which are simple as in most Chilocorini), and most importantly in the form of the clypeus and genal lobes. The clypeus is not more or less deeply emarginate without a marginal bead, as in most other Chilocorini, but is straight across the front, without a trace of an emargination, and with a strong marginal bead. The genal lobes are as in most other Chilocorini, not suddenly contracted at the inner margin of the eye. When more of the Australasian "*Orcus*" are thoroughly studied, it may seem best to establish *O. ovalis* as the type of a distinct genus.

ORCUS Mulsant

Orcus Mulsant, 1850, Species Trimères Sécuripalpes, p. 465; Crotch, 1874, Revision of the Coccinellidae, p. 188; Weise, 1923, Arkiv Zool., 15(12):133.

Type species. Orcus janthinus Mulsant, by subsequent designation of Crotch, 1874.

Chilocorini with form nearly circular, moderately convex, upper surface glabrous. Antenna eight-segmented; first segment slightly curved, less than twice as long as wide, constricted at basal third, apex with a small, rounded lateral lobe; second barrel-shaped, a little longer than wide; third obconical, much narrower at base than apex of second, less than twice as long as wide; fourth through seventh mutually similar in shape but becoming progressively longer and wider; seventh somewhat oblique at apex; eighth nearly twice as long as wide, rounded acuminate. Mandible heavy, subangulate at middle of outer margin. Terminal segment of maxillary palp stout, subsecuriform, the apex strongly oblique; lacinia with three or four short, stout spines on outer face. Terminal segment of labial palp cylindrical, slightly tapering, twice as long as wide at

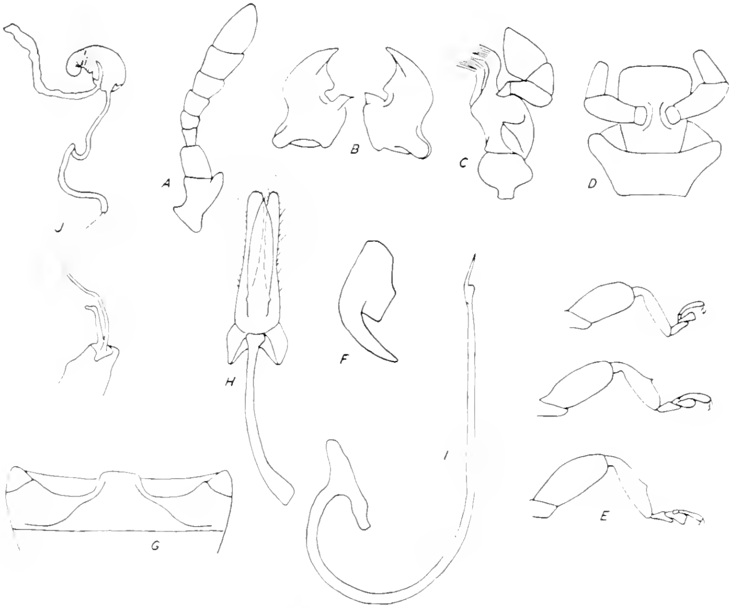

FIG. 14. *Orcus janthinus* Mulsant.

base. Prosternal lobe moderately broad, truncate at apex. Pronotum finely margined across median third of base. Elytra with lateral margins slightly reflexed, epipleura weakly foveolate for the reception of the femoral apices. Abdomen similar in both sexes, each with five visible sternites, the fifth evenly rounded. Metacoxal arcs broadly open, the line running parallel to the posterior margin of the sternite, nearly to the lateral margin. Legs with femora moderately stout; tibiae excavate in apical half or more for the reception of the tarsi; tarsal claws strongly curved, each with a large quadrate, plate-like tooth in basal half. Male genitalia: median lobe long, lanceolate, not visibly asymmetrical apically; parameres slender, straight, not broadened in apical half, slightly longer than median lobe; trabes longer than median lobe; sipho rather slender, terminating in a slender, acute spine. Female genitalia: receptaculum seminis a stout body with nodulus indicated by a slight prominence, ramus not defined, cornu strongly curved and broadly rounded at apex, accessory gland much longer than receptaculum; sperm duct with parts nearly equal in length, the thick section about three times the diameter of the thin section; infundibulum present; hemisternites slender, three times longer than wide at base, styli button-shaped, each with two or three long setae.

Orcus janthinus is a large species, 5.0-5.7 mm, uniformly steel-blue above with the exception of the reddish-yellow labrum. Beneath, the meso- and metathoraces and legs are castaneous, the antennae and abdomen reddish-yellow. The series studied is from Bogor, Java, taken in February, 1954, by Mr. O. D. Deputy. I have seen no other species of this genus.

ANISORCUS Crotch

Anisorcus Crotch, 1874, Revision of the Coccinellidae, p. 190; Weise, 1902, Termes. Füzetek, 25:508.

Type species. Anisorcus fryi Crotch, by original designation.

Chilocorini with form broadly oval, moderately convex, upper surface glabrous. Antenna seven-segmented; first segment short, bent, hardly constricted; second barrel-shaped, of same diameter and as long as the first; third obconical, shorter than and much narrower than second; fourth and fifth mutually similar in shape, the fifth slightly wider and longer than the fourth but shorter than the third; sixth similar in shape to the second and slightly longer; seventh nearly twice as long but not quite as wide as sixth, cylindro-acuminate, the apex rounded. Mandibles moderately stout, the inner margin of the right mandible with a small tooth just in front of the notch, outer margins broadly rounded, apices acute. Terminal segment of maxillary palp cylindrical, tapering slightly toward apex which is oblique but not strongly so; lacinia with a patch of nine or ten stout spines on outer side. Terminal segment of labial palp cylindro-acuminate, twice as long as wide at base. Prosternal lobe moderately broad, truncate at apex. Pronotum without fine marginal line across base. Elytra with lateral margins slightly reflexed, very finely beaded; epipleura shallowly foveolate for the reception of the femoral apices. Abdomen alike in both sexes, each with six visible sternites, the fifth sternite in each is truncate. Metacoxal arcs nearly straight from intercoxal process nearly to posterior margin of sternite where they turn abruptly and follow margin nearly to lateral margin of sternite. Legs with femora not noticeably stout; the tibiae rather broad and short; tarsal claws each with a strong tooth in basal half. Male genitalia: median lobe elongate triangular, not noticeably asymmetrical apically; parameres very broad, not constricted in

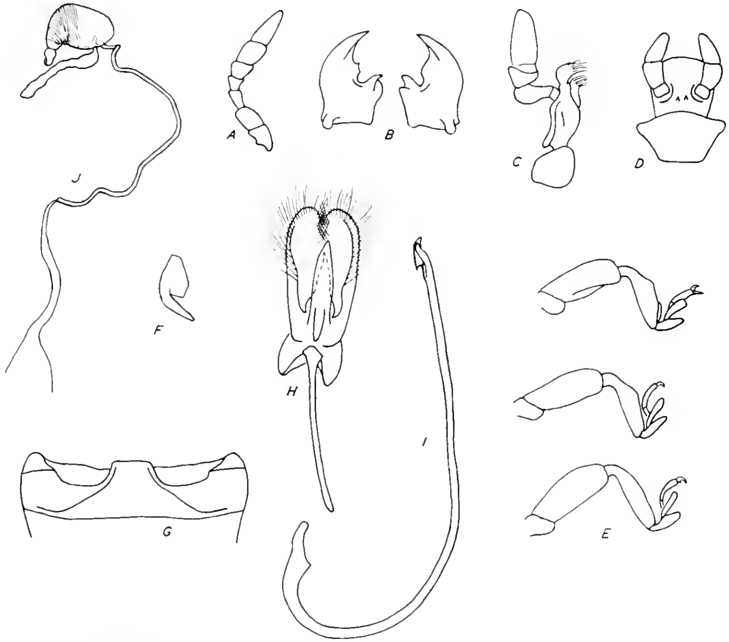

FIG. 15. *Anisoreus fryi* Crotch.

basal half, one-third longer than median lobe; trabes slender, as long as main portion of the aedeagus; sipho rather slender, the siphonal capsule poorly developed, apex of sipho slightly recurved and covered by a membraneous hood. Female genitalia : receptaculum seminis with a very stout body, nodulus and ramus not defined, cornu very short and ends in a flat, rounded appendix, accessory gland only a little longer than receptaculum; sperm duct in two parts, the thick section is of even diameter throughout and only slightly thicker than the thin section at or near the junction of the two sections; the thin section, normally thin throughout its length, remains of small diameter for but a short distance, then gradually enlarges its diameter until it joins the bursa copulatrix; infundibulum absent; hemisternites very elongate triangular, rounded at tips, styli apparently absent.

Anisorcus fryi is a species of below medium size, 3.0-3.2 mm, piceous black above except for head, pronotum, and narrow lateral margins of the elytra which are reddish-yellow. The under parts are uniformly reddish-yellow. The structure of the female genitalia apparently indicates a relationship with *Chilocorus* and *Phaenochilus.* The series before me comes from Suva, Fiji Is., taken in March 1960 by Mr. N. L. H. Krauss. Two other species were included in this genus at the time of description; I have seen neither of them.

CHILOCORUS Leach

Chilocorus Leach *in* Brewster, 1815, Edinburgh Encyclopedia, 9:116; Redtenbacher, 1843, Tentamen dispositionis Coleopterorum pseudotrimerorum, p. 11; Reprint of above in Germar, 1844, Zeitsch. f. Ent., 5:118; Mulsant, 1850, Species Trimères Sécuripalpes, p. 452; Crotch, 1874, Revision of the Coccinellidae, p. 183; Gorham, 1892, Biol. Centr.-Amer. Ins., Coleopt., 7:175.

Type species. Coccinella cacti Linné, monobasic.

Chilocorini with form broadly oval, strongly convex, upper surface glabrous except for a few hairs on the flanks of the pronotum. Antenna eight-segmented; first segment elongate, subcylindrical, slightly bent, more than twice as long as wide at widest part; second nearly equilateral, dome-shaped, greatest width near base, rounded in apical third; third wedge-shaped, apex twice as wide as base and wider than length; fourth nearly quadrate, one-third wider than long; fifth through eighth forming a fusiform club, fifth and sixth each equal in length to fourth, each wider at apex than at base, seventh slightly longer and wider than sixth, eighth conical, half again as long as seventh but slightly narrower, slightly excavate on one side near apex. Mandible stout, apex slender, outer margin subangulate near middle. Terminal segment of maxillary palp with lateral margins nearly parallel, apical margin strongly oblique, lacinia with a patch of eight stout spines on outer face. Terminal segment of labial palp elongate subconical, slightly more than twice as long as wide at base. Prosternal lobe flat, moderately wide. Elytral margins not reflexed, finely beaded; epipleura shallowly foveolate for the reception of the femoral apices. Abdomen with six visible sternites in male, five in female; metacoxal arcs in form of a quarter circle, merging with the posterior margin of the sternite; margin of fifth sternite transverse, straight, of sixth slightly emarginate in male, margin of fifth evenly rounded in female. Legs with stout femora, tibiae with a triangular tooth on each at basal third, tarsal claws with small, quadrate tooth on each at base. Male genitalia : median

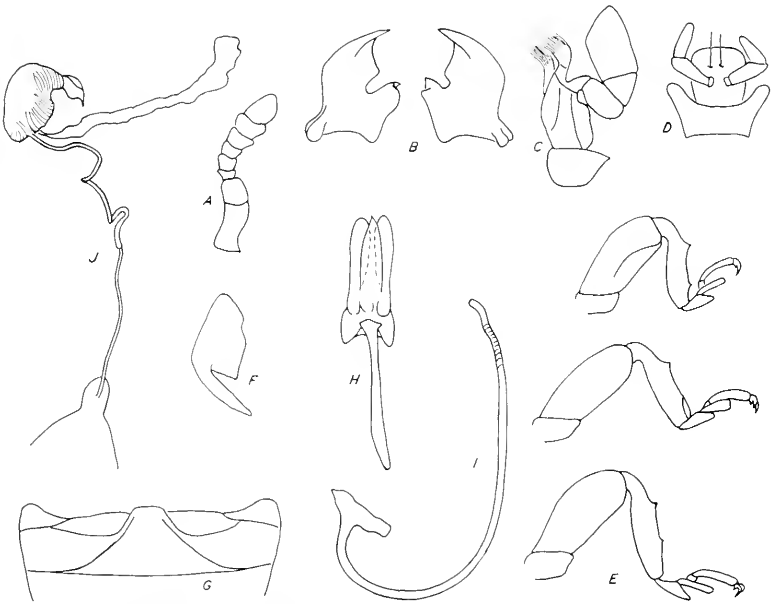

FIG. 16. *Chilocorus cacti* (Linné).

lobe very slightly asymmetrical, elongate triangular with sides gently curved; parameres hardly longer than median lobe, moderately stout; trabes slender, longer than the main parts of the aedeagus; sipho moderately stout, of even diameter throughout most of its length, near apex it is twisted through a quarter turn, apex truncate. Female genitalia: receptaculum seminis a stout body without differentiation into nodulus and ramus, cornu very short and bent, with a falciform appendix at apex, accessory gland very long and slender; sperm duct long, in the usual two sections, the thick section only slightly thicker than the thin section; infundibulum absent, replaced by a fleshy, unpigmented protuberance; hemisternites rather broadly triangular.

Chilocorus Leach is very closely related to *Egius* Mulsant, a monobasic West Indian genus and also to *Phaenochilus* Weise of the Malayan region. The absence of tibial spurs and the worldwide distribution of the species of *Chilocorus* suggests that the Old World is the original home of the genus. *Chilocorus* is a large genus, with many species in the Palaearctic and Ethiopian regions, fewer in the Indo-malayan, still fewer in the Nearctic, Neotropical and Australian regions. A thorough study of the species would probably result in the splitting of the genus.

EGIUS Mulsant

Egius Mulsant, 1850, Species Trimères Sécuripalpes, p. 464.
Chilocorus, — Crotch, 1874, Revision of the Coccinellidae, p. 188 (part).
Type species. Egius platycephalus Mulsant, monobasic.

Chilocorini with form nearly circular, flattened convex, upper surface glabrous. Antenna eight-segmented; first segment short and stout, nearly equilateral; second longer than first but of equal width, slightly narrower at apex than at base; third less than half as long as second, twice as wide at apex than at base; fourth similar in shape to third but longer and wider; fifth a little shorter but about as wide as fourth; sixth similar in shape to fifth but a little wider; seventh longer than wide, a little longer than sixth; eighth longer than seventh, tapering to a rounded apex. Mandibles stout, apices rather blunt, outer margin feebly concave in basal half, nearly straight in apical half. Terminal segment of maxillary palp long and narrow, tapering, apex slightly oblique; lacinia with a row of six or seven short, stout spines parallel to the row of longer setae. Terminal segment of labial palp elongate conical, rounded at apex. Prosternal lobe moderate in width, rounded at apex, the margins with a strong bead. Elytral margin not reflexed, with a fine marginal bead in basal third, epipleura not foveolate for the reception of the femoral apices. Abdomen with six visible sternites in both sexes; metacoxal arcs joining the posterior margin of the sternite near the lateral margin. Legs rather stout; femora not inflated; tibiae with a triangular tooth on outer margin at middle of length; tarsi broad, tarsal claws each with a feeble basal tooth. Male genitalia: median lobe elongate triangular, slightly asymmetrical near apex, side margins nearly parallel in basal half; parameres flattened, not constricted in basal half, slightly shorter than median lobe; trabes moderately stout, equal in length to median lobe; sipho rather slender, the apex twisted. Female genitalia: receptaculum seminis and accessory gland similar to those parts in *Chilocorus;* sperm duct with slender section very thin, total length of duct proportionately longer than in *Chilocorus;* infundibulum absent, replaced by a fleshy protuberance on the

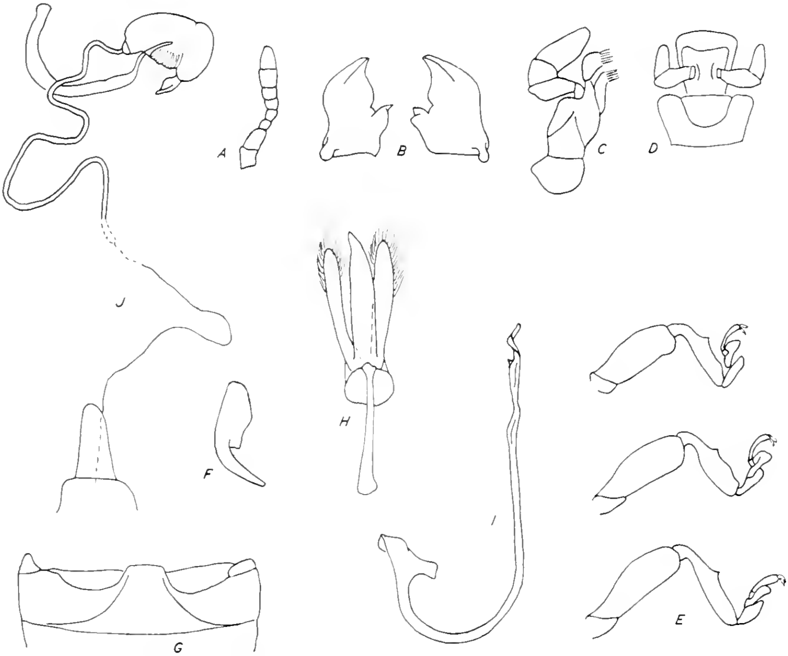

FIG. 17. *Egius platycephalus* Mulsant.

bursa copulatrix; hemisternites short, rather broad, somewhat crescent-shaped, styli apparently absent.

The type and only species of this genus is found on Cuba. While anatomically very close to *Chilocorus*, its superficial appearance is very different from that of any of the recorded species of *Chilocorus*. The very strongly alutaceous surface of the head and elytra, and the almost iridescent metallic greenish-purple color of the elytra set it apart immediately.

PHAENOCHILUS Weise

Phaenochilus Weise, 1895, Ann. Soc. Ent. Belgique, 39:135; 1913, Philippine Journ. Sci., 8, D:241.

Type species. Phaenochilus punctifrons Weise, by subsequent designation of Korschefsky, 1932.

Chilocorini with form nearly circular, strongly convex, upper surface glabrous. Antenna eight segmented; first segment short, stout, curved; second longer and thicker than first, much narrower at apex than at base; third nearly twice as long as wide at base, apex half again as wide as base; fourth to sixth mutually similar in shape, fourth and fifth nearly equal, seventh slightly

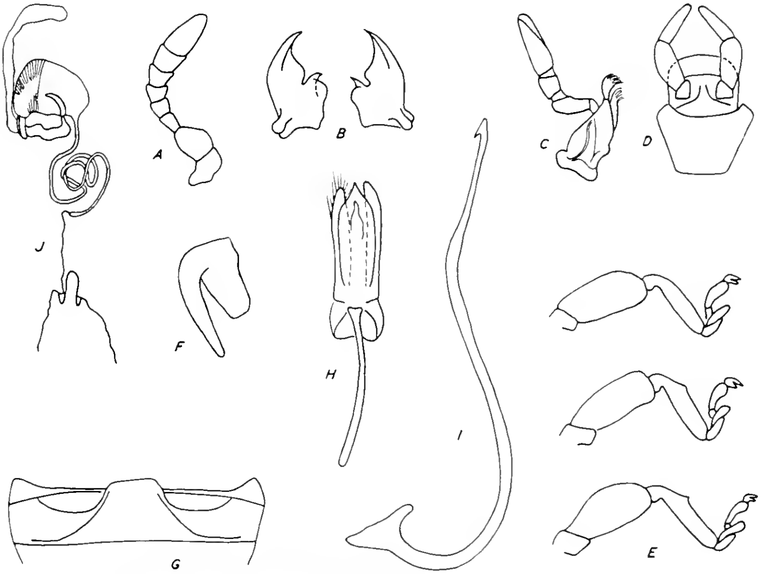

FIG. 18. *Phaenochilus punctifrons* Weise.

longer and wider than fifth; eighth twice as long as sixth, tapering to a blunt point. Mandible somewhat longer than broad, outer margin not strongly curved, apex rather elongate and slender. Maxillary palp long and slender, the terminal segment very long, about three times longer than wide, tapering to a blunt point; lacinia with a patch of about seven stout spines on outer face. Terminal segment of labial palp slender acuminate, rounded at apex. Prosternal lobe moderately wide, convex, rounded at apex, the lateral margins beaded, the bead continued partly around the anterior coxal cavities. Margins of elytra strongly reflexed, with extremely fine marginal bead; epipleura shallowly foveolate for the reception of the femoral apices. Abdomen with six visible sternites in male, the fifth sternite broadly truncate, five in female, the fifth broadly rounded. Metacoxal arcs run outward and back nearly to the posterior margin of the sternite, thence following the margin nearly to the lateral margin of the abdomen. Legs rather short; femora moderately stout; tibiae slender, those of legs II and III with triangular tooth at the top of the tarsal groove, that on leg III stronger than that on leg II; terminal segment of tarsus stout, claws stout, the apical half at nearly a right angle to the basal half, the basal tooth elongate, parallel to and nearly as long as the apical half of the claw. Male genitalia: median lobe equal in length to the parameres, widest at apical third, side margins straight in basal two-thirds, apical third triangular, apex acutely pointed; parameres paddle-shaped, not noticeably constricted basally, apices bluntly rounded; trabes slender, longer than the median lobe; sipho rather slender, of even diameter in first four-fifths, apical fifth much more slender and ending in a harpoon-shaped point. Female genitalia: receptaculum seminis very stout, much like that of *Chilocorus*, appendix of cornu strongly developed, accessory gland somewhat longer than long diameter of the receptaculum; sperm duct with thick portion more than twice as long as the very thin portion; infundibulum absent, replaced by a fleshy tab at apex of bursa copulatrix; hemisternites moderately long, triangular, styli not prominent, appearing as pits near apices of these sclerites, each pit furnished with two or three long setae.

This small genus of three species, *P. punctifrons* Weise, *P. ruficollis* Weise, and *P. monostigma* Weise, is at home in the Indomalayan region from Java to Mindanao in the Philippines. Specimens of all three species are in my hands. The genus may be immediately recognized by the long, slender maxillary palps and the broadly reflexed elytral margins.

TRICHORCUS Blackburn

Trichorcus Blackburn, 1892, Trans. Proc. Roy. Soc. South Australia, 15:73.
Type species. Trichorcus cinctus Blackburn, monobasic.

The original diagnosis is quoted in full below.

"Trichorcus (gen. nov. Coccinellidarum) Ab *Orco* differt corpore haud metallico, subopaco, dense pubescenti.

I can find no structural character to distinguish the genus from *Orcus*, but it seems scarcely possible to place in that genus a non-metallic subopaque species densely clothed with pubescence."

From the description of the type species little of importance can be learned except that the individuals of this species are a trifle wider than long. It will be necessary to study specimens of this species in order to disclose its relationships.

CHILOCORUS (TRICHOCORUS) Sicard

Chilocorus (*Trichocorus*) Sicard, 1921, Bull. Soc. Portugaise Sci. Nat., 8:213; Mader, 1954, Explor. Parc Nat. Albert, Mission de Witte, Lief. 80, Coccinellidae, pars III, p. 80.
Type species. Chilocorus pilosus Sicard, by present designation.

It is not possible to place this taxon in its proper position in the tribe from the information contained in the above references. Two species were included in the original description and these differ in the formation of the anterior tibiae. The type species is said to have angulate but not spinose tibiae, a very small scutellum, upper surface clothed with somewhat long, gray pubescence, elytral margins not at all reflexed, basal margin of pronotum sinuate either side of the scutellum, and other characters mostly relating to color.

Unfortunately, through a misreading of the original description, Dr. Mader has introduced a false character into his key. Sicard states that the pubescence is "dirigée en avant" on the pronotum only, on the elytra it is "dirigés (*sic!*) en arrière."

CORYSTES Mulsant

Corystes Mulsant, 1850, Species Trimères Sécuripalpes, p. 506; Crotch, 1874, Revision of the Coccinellidae, p. 208; Chapuis, *in* Lacordaire, 1876, Gen. Coleopt., 12:244, 249; Gorham, 1894, Biol. Centr.-Amer., Ins., Coleopt., 7:182; Weise, 1899, Deutsch. Ent. Zeitsch., p. 269, 1903, *ibid.*, p. 208; 1904, *ibid.*, p. 358; 1927, Arkiv f. Zool., 18A(4), no. 34, pp. 12-13.

Type species. Corystes hypocrita Mulsant, monobasic.

Mulsant, 1850, placed his new genus *Corystes* in the third branch, Thalassaires, of his Hyperaspiens. He took note of the fact that the structure of the anterior part of the head was different from that of his Chilocoriens in that in *Corystes* there is a break in continuity between the clypeus and genal lobes and no break in other Chilocoriens.

Crotch, 1874, agrees with Mulsant in placing *Corystes* near *Thalassa* but brings these genera to the beginning of his Hyperaspides, directly following his group, Chilocorides.

Chapuis, 1876, removed the genus from his Hyperaspites and placed it as a transitional form in the Chilocorites. However, he noted, as Mulsant had before, that the structure of the head is not typically chilocorine and that otherwise the characters of the genus are largely hyperaspine.

Gorham, 1894, added little to the clarification of the problem. He accepted Chapuis' findings and continued *Corystes* in the Chilocorini.

Weise, 1899, working with specimens which he believed at the time were *Corystes hypocrita*, returned the genus to the Hyperaspini. In 1903, he added a second species to the genus, noting that the structure of the head of the new species was somewhat different from that of the original species. In 1904, Weise again asserts that the genus is undoubtedly hyperaspine.

In 1927, in a posthumous paper, Weise reverses himself on the ground that the species dealt with in 1899, 1903, and 1904, were misidentified. In this paper, he sets up a new genus, *Diazonema*, type *D. fallax* Weise (*Corystes hypocrita* Weise, not Mulsant, renamed), in the Hyperaspini and redescribes *Corystes hypocrita* Mulsant from specimens from San Fermin, Bolivia. He now places *Corystes* in the Chilocorini but notes the difference between it and the rest of the Chilocorini in the structure of the clypeus and genal lobes.

I have before me a short series of a species from Colombia which I am convinced represents an undescribed species of *Corystes*. There is no question in my mind that the species does belong in the Hyperaspini near *Thalassa*. The antenna with the antepenultimate segment very long, the mandible with a second tooth very near the apex, the male genitalia with a depressed, strongly asymmetrical median lobe, and other characters are all foreign to the Chilocorini but common to all Hyperaspini known to me.

ELPIS Mulsant

Elpis Mulsant, 1850, Species Trimères Sécuripalpes, p. 449; 1866, Monographie des Coccinellides, pp. 283, 291; Crotch, 1874, Revision of the Coccinellidae, p. 181; Chapuis *in* Lacordaire, 1876, Gen. Coleopt., 12:191, 193; Sicard, 1909, Ann. Soc. Ent. France, 78:64, 82; Korschefsky, 1932, Coleopt. Catalogus (Junk), pars 120, Coccinellidae, p. 248; Mader, 1941, Explor. Parc Nat. Albert, Mission de Witte, fasc. 34, p. 185; 1954, *op. cit.*, fasc. 80, pp. 117, 118.

Type species. Elpis dolens Mulsant, monobasic.

The above are all the references to *Elpis* that I have been able to find in the literature. All of the authors, except Korschefsky, agree in placing this genus in the Coccinellini, near *Menochilus*. I have examined a specimen of the type species and it is obvious that the genus does belong in the Coccinellini. Korschefsky gave no explanation for placing the genus in the Chilocorini.

(Received 8 December 1964.)

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COMMENTS ON SOME RECENT CHANGES IN THE CLASSIFICATION OF THE CIIDAE (COLEOPTERA)

By

John F. Lawrence

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
October 20, 1965

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Fishes of the Gulf of Maine, by Henry B. Bigelow and William C. Schroeder. Washington, viii - 577 pp., 1953. Photo-offset reprint, $6.50.

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No. 5 — *Comments on Some Recent Changes in the Classification of the Ciidae (Coleoptera)*

By

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Musum of Comparative Zoology, Harvard University, Cambridge, Mass.

The family Ciidae includes at present 40 genera and about 550 species. The group has been badly neglected in the past, and although a few excellent local monographs have appeared, the last treatment of the world fauna was published in 1848. The European fauna has probably been more extensively studied than that of any other area, but most of the workers have not been specialists and have tended to be provincial in their approach, completely ignoring, for instance, the contributions to the Holarctic fauna made by Japanese and Americans. Lohse (1964) produced a short paper in which some of the European generic concepts were reexamined and 3 new generic group names proposed. This recent contribution is certainly welcome, since it represents the first step in clarifying the relationships within this difficult group. In the present discussion, I will review Lohse's proposals and reevaluate his concepts in the light of my own work on the North American Ciidae. Since the histories of the various European generic names have been discussed previously, it may seem redundant to include them here; I think this is justified, however, considering that even Lohse overlooked or misinterpreted some of these historical facts.

1. *ENTYPUS*, *RHOPALODONTUS*, AND *SULCACIS*

Although the genera *Entypus* and *Rhopalodontus* represent distinct taxa whose species are only distantly related, the nomenclatural histories of the two names are so interwoven that it seems practical to discuss them together. *Ropalodontus* Mellie (justifiably emended to *Rhopalodontus* by Gaubil, 1849) was first proposed in 1847 for the species *Cis perforatus* Gyllenhal, the main diagnostic character being the expanded, rounded, and externally spinulose protibial apices. In the same year, Redtenbacher described *Entypus*, which included only the species *Cis affinis* Gyllenhal (misidentified as *Apate fronticornis* Panzer), characterized by having 9-segmented antennae, with the 3rd segment longer than the following 3 together, and spinulose protibial apices. In the following year, Mellie included *C. affinis* in his genus *Enncarthron,* which had been described some months prior to the publication of Redtenbacher's work, and placed *Entypus* in synonymy. Mellie included the true *A. fronticornis* in the genus *Cis*, primarily because of its 10-segmented antennae.

Thomson (1863) considered *Rhopalodontus* and *Orophius* Redtenbacher (=*Octotemnus* Mellie) to be so different from other members of the family that he included them in a separate tribe, the Orophiina. Being a careful worker, he found several other characters which consistently distinguished the group, such as the conical, projecting, and subcontiguous procoxae, short prosternum, deep antennal sulci, and subequal 3rd and 4th antennal segments. In the same paper, Thomson noted the close similarity between *Enncarthron affine* (Gyllenhal) and *Cis fronticornis* (Panzer), and in spite of the difference in antennal segmentation, he placed them both in *Entypus*. Mellie's name *Ennearthron* could not be applied, because a very different species, *Cis cornutus* Gyllenhal, had been designated as its type by Demarest (1860). Kiesenwetter (1877) included *Entypus* as a distinct subgenus of *Cis* and added to it a third species, *Ennearthron wagai* Wankowicz, which had been described as having spinulose protibial apices. He considered the Orophiina to be a separate family, the Orophyidae, to which he added *Xylographus* Mellie. A more extreme view was taken by Seidlitz (1872), who placed these genera in a tribe of the family Anobiidae.

In spite of the efforts of Thomson and Kiesenwetter, most European entomologists chose to ignore these two concepts and to rearrange the above species according to more superficial characters, such as the number and relative lengths of antennal segments. Thus, Jacquelin Du Val (1861) placed *C. fronticornis* in the genus *Rhopalodontus* in spite of its totally different procoxal structure, and returned *affinis* to *Enncarthron,* because of its 9-segmented antennae. In 1915, Peyerimhoff placed *Cis bicornis* Mellie in *Rhopalodontus* on the basis of antennal and protibial characters only, and Nobuchi (1960a) described 2 more species, *R. japonicus* and *R. tokunagai*, which also appear to be in the *fronticornis* group. Until quite recently, then, the genus *Rhopalodontus* contained two distinct and distantly related groups of species: those resembling *Enncarthron affine* and belonging properly to *Entypus* of Redtenbacher and Thomson, and those resembling *R. perforatus*.

The situation was clarified by Lohse (1964), who had restudied the European species carefully enough to recognize the true relationships. By reviving the concept of Redtenbacher and Thomson and uniting *E. affine*, *R. fronticornis*, and *R. bicornis* into a single genus, he not only called attention to the apparent affinities of these three species, but also eliminated discordant elements from both *Ennearthron* and *Rhopalodontus*. In addition to the above, Lohse added *Cis bidentulus* Rosenhauer to the group. Because of the variation in antennal segments, he proposed the subgenus *Entypocis* (with *C. bidentulus* as its type) for those species with 10-segmented antennae, leaving *Entypus affinis* the only member of the nominate subgenus. *Ennearthron wagai* Wankowicz (1869) (mis-cited in Lohse as *E. wagai* Wanka) was placed in a new genus, *Wagaicis*, because of its very narrow and laminate prosternal process.

I agree with Lohse's revival of *Entypus* and his inclusion of the 4 European species. In my own studies of North American Ciidae, I have encountered two more species, *Cis curtulus* Casey and *Sulcacis lengi* Dury, which also belong to this group. I have compared these with specimens determined as and fitting the descriptions of *E. fronticornis*, *E. affinis*, and *E. bidentulus*. *C. curtulus* is very similar to *E. bidentulus*, while *S. lengi* is unique in having 9-segmented antennae, a somewhat shortened prosternum, and no sexual modifications on the head of the male. Since *lengi* is here selected as the type of *Sulcacis* Dury (1917), this genus becomes a junior synonym of *Entypus*. I would tentatively add *R. japonicus* and *R. tokunagai*, both from northern Japan, to this genus, on the basis of descriptions and illustrations. I do not think the proposed division into subgenera is necessary, especially if it is based on the number of antennal segments.

There is one final matter that appears to have been overlooked by all of the workers in the Ciidae. This is the fact that the name *Entypus* was not available when used by Redtenbacher, having already been applied to a pompilid wasp (Hymenoptera) by Dahlbom (1843). *Entypus* is a primary junior homonym and must be replaced. Of the two remaining available names which have been applied to the group, *Sulcacis* Dury is the oldest and is here considered as a replacement name. Although *Sulcacis lengi* Dury is the most atypical member of the group, it becomes the type species because of the priority of the generic name. I do not think that *S. lengi* is distinct enough to be placed in a separate genus; if this species were to be removed from the group, however, then Lohse's *Entypocis* is the next oldest available generic name and *E. bidentulus* would be considered the type.

A synonymy and redefinition of *Sulcacis* is given below.

SULCACIS Dury

Sulcacis Dury, 1917, Jour. Cincinnati Soc. Nat. Hist., 22(2):20; Leng, 1920:247. Type, by present designation, *Sulcacis lengi* Dury, 1917:21.

Entypus Redtenbacher, 1847, Faun. Austr., (3):350 (*non* Dahlbom, 1843:35); Thomson, 1863:193; Sahlberg, 1926:78; Lohse, 1964:118. Type, by monotypy, *Cis affinis* Gyllenhal, 1827:628 (misidentified as *Apate fronticornis* Panzer).

Cis (*Entypus*), Kiesenwetter, 1877:190; Reitter, 1878:21.

Entypus (*Entypocis*) Lohse, 1964, Ent. Blätter, 60(2):121. Type, by original designation, *Cis bidentulus* Rosenhauer, 1847:58.

Cis (in part), Gyllenhal, 1827:624; Mellie, 1847:109; Mellie, 1848:236; Lacordaire, 1857:551; Jacquelin Du Val, 1861:237; Seidlitz, 1872:44; Abeille de Perrin, 1874:19; Reitter, 1878:27; Seidlitz, 1891:282; Casey, 1898:78; Schilsky, 1900:37E; Reitter, 1902:47; Dalla Torre, 1911:5; Dury, 1917:5.

Ennearthron (in part), Mellie, 1848:360; Lacordaire, 1857:552; Jacquelin Du Val, 1861:238; Abeille de Perrin, 1874:80; Reitter, 1878:30; Schilsky, 1900:37B; Reitter, 1902:59; Dalla Torre, 1911:23; Nobuchi, 1960a:41.

Rhopalodontus (in part), Jacquelin Du Val, 1861:238; Abeille de Perrin, 1874:76; Reitter, 1878:30; Schilsky, 1900:37D; Reitter, 1902:57; Dalla Torre, 1911:21; Peyerimhoff, 1915:26; Nobuchi, 1960a:39.

Form oblong to elongate, strongly convex and cylindrical; vestiture short, usually dual, consisting of both erect and inclined bristles. Head moderately declined, partly covered by pronotum; frontoclypeal ridge of male usually with 2 small teeth or tubercles; antennal fossa relatively deep. Antenna 9- or 10-segmented, with 3-segmented club; segments III and IV subequal, or III longer than next 2 combined; maxillary palp narrow and elongate. Pronotum somewhat constricted anteriorly, narrowly margined laterally; anterior edge usually simple in both sexes. Elytra with relatively coarse, indistinctly dual, uniform or seriate punctation. Prosternum slightly tumid, concave laterally, slightly shorter than intercoxal process which is narrow but not laminate. Protibia expanded at apex, outer apical angle forming a rounded process bearing several small spines. Metasternum convex, the suture short. Meso- and metatibiae slightly expanded and spinulose at apex. Sternite III of male with median pubescent fovea.

A small genus with species throughout the Holarctic region. Intermediate in its characters between *Cis* and *Eridaulus*, on the one hand, and *Ceracis*, *Wagaicis*, and *Malacocis* on the other, differing from the former by the spinulose protibial apices and from the latter by the broader intercoxal process. The species which have been studied biologically occur primarily on fungi of the *Polyporus versicolor* group (Paviour-Smith, 1960).

2. *HADRAULE*, *ERIDAULUS*, AND *XESTOCIS*

Two of Thomson's genera, *Hadraule* and *Eridaulus*, have been involved in considerable taxonomic confusion over the past 100 years. Lohse (1964), in his analysis of the problem, has referred to it as a "nomenklatorischen Tragikömodie," an opinion with which I am inclined to agree.

Hadraule was originally proposed for the species *Cis elongatulus* Gyllenhal, characterized by the somewhat flattened body form, subquadrate prothorax, well-separated procoxae, and regularly striato-punctate elytra. Seidlitz (1872), Kiesenwetter (1877), and Reitter (1878) considered it to be a subgenus of *Cis*. Schilsky (1900) first expanded the subgenus to include certain other species with a more or less parallel form, subquadrate prothorax, and elytra with rows of setae alternating with rows of large punctures. In addition to *C. elongatulus* (misspelled as *elongatus* in text, p. 59), he placed *Cis setifer* Reitter and *Cis striatulus* Mellie within *Hadraule*. Reitter (1902) continued the trend by including the following species as well: *C. seriatopilosus* Motschulsky, *C. heiroglyphicus* Reitter, *C. bifasciatus* Reitter, *C. comptus* Gyllenhal, *C. coriaceus* Baudi, and *C. pumilio* Baudi. Jacobson (1915) doubtfully placed *Cis fuscipes* Mellie, described from North America and Madeira, in the same group. Roubal (1936), having examined the type of *C. elongatulus* and discovered that it had 9-segmented, rather than 10-segmented, antennae, transferred the subgenus (including only the type species) to the genus *Ennearthron* Mellie. Through a misunderstanding of the rules of nomenclature, Roubal replaced *Hadraule* with a new name, *Knablia*. Lohse (1964) restored *Hadraule* and suggested that it be used in the original sense, as a separate genus including only the type species, *Hadraule elongatula*. Lohse further stated that *Cis comptus* and its relatives should be placed in the subgenus *Eridaulus*. This is entirely wrong, being based on an erroneous type designation, as will be explained below. The rest of the species mentioned above do seem to form a natural group, to which the American species *Cis falli* Blatchley, *Cis striolatus* Casey, and *Cis versicolor* Casey might be added. *H. elongatula* shows a marked similarity to members of the *C. comptus* group and also to *Maphoca blaisdelli* Casey, the latter differing mainly in the number of antennal club segments.

The genus *Eridaulus* Thomson (1863) originally included two species, *Anobium nitidum* Fabricius and *Cis jacquemarti* Mellie, which were characterized by the 10-segmented antennae, reflexed "gular margin," elytra with larger and smaller punctures (dual punctation), short, carinate prosternum, and produced and dentate protibial apices. Seidlitz (1872), Sahlberg (1926), and a few others retained it as a genus, but most later authors reduced it to a subgenus of *Cis*. Seidlitz added *Cis glabratus* Mellie and *C. lineatocribratus* Mellie, and Schilsky (1900) included *C. quadridens* Mellie as well. Roubal added one more European species, *Cis bituberculosus* Roubal, 1937 (=*Cis bituberculatus* Roubal, 1912, *non* Gorham), and in recent years Chujo (1940), Miyatake (1954), Nakane and Nobuchi (1955), and Nobuchi (1955, 1960b) have described several others from Japan. The only worker to designate a type for *Eridaulus* was Abeille de Perrin (1874), who selected *Cis comptus* Gyllenhal. This species, however, was not originally included in the genus, and is therefore unavailable as a type. In the same work, Abeille de Perrin designated *C. nitidus* as the type of *Entypus*, making a similar error. The name *Eridaulus*, then, is still available for the *Cis nitidus* group, contrary to the statement of Lohse (p. 119), and the type must still be designated. Since I have not examined the type specimens of either *C. nitidus* or *C. jacquemarti*, I hesitate to select one of them as the type at the present time.

In the past several years, I have examined specimens of Ciidae from various parts of the world, and it has become apparent to me that a number of other species described in *Cis* and the majority of those included in *Xestocis* Casey should be placed in *Eridaulus*. Casey (1898) proposed the genus *Xestocis* for 5 North American species with a carinate prosternum. Dury (1917), Brèthes (1922), and Hatch (1962) added 14 more species, and most of those examined fall within this group. Since a type has not been selected for *Xestocis*, I here designate *X. levettei* Casey, the best known of the American species. Miyatake (1954) noted the similarity of *X. levettei* to *Cis* (*Eridaulus*) *konoi* Chujo, and I have noticed the resemblance of the former to *C. nitidus*, with respect to dual elytral punctation, carinate prosternum, dentate protibial apices, secondary sexual characters, male genitalia, and larval urogomphi. I think there is little doubt that *Xestocis* should be considered a junior synonym of

Eridaulus. Since a number of species synonymies and new generic combinations are involved, I will not present here a complete list of American forms to be included in *Eridaulus*, but will publish this separately in a forthcoming revision of the New World species. In addition to the American forms, several species of *Cis* from the Pacific region, such as *Cis pacificus* Sharp (Hawaii) and *C. agariconae* Zimmerman (Micronesia) should be placed in the genus.

Although *Eridaulus* appears to be quite close to the genus *Cis*, I think it should be given generic rank for several reasons. According to Mayr, Linsley, and Usinger (1953), the size of the gap between two genera should be inversely proportional to the sizes of the groups involved. With its present constitution, the genus *Eridaulus* is large enough, both in numbers of species and in extent of distribution, to warrant generic distinction. There are about 30 named species, and several more apparently undescribed, extending throughout the Holarctic region and as far south as New Zealand in the Pacific area. Furthermore, within the genus, several distinct subgroups can be recognized, and certain independent character trends can be followed. Finally, the group displays a biological unity, most of the species being associated with the larger, woody fruiting bodies of fungi such as *Fomes* and *Ganoderma*. This habit, which has been independently evolved in several unrelated genera, such as *Ceracis* and *Xylographus*, may be associated with structural modifications, such as the prosternal carination and convex form of the adult and the increased molar area in the larval mandible. Paviour-Smith (1960) noted that the "headquarters" of *E. nitidus* was the fungus *Ganoderma applanatum*, although the beetle was recorded from several other fungi, and this is quite similar to the host range and headquarters of the American *E. levettei*. Saalas (1923) reported *E. quadridens*, *E. lineatocribratus*, and *E. jacquemarti* from *Fomes pinicola*, and the Japanese species *E. rufocastaneus* and *E. nikkoensis* have been taken on the same fungus. *E. biarmatus* (Mannerheim) and several *Eridaulus* from western North America occur on *Fomes pinicola*, *F. annosus* and related fungi. In Hawaii, where most of the Ciidae are collected by beating dead vines and branches, *E. pacificus* is the only species which has been reported feeding on the woody bracket fungi. It appears to me, then, that the members of this group represent a morphologically and biologically distinct genus, to which the name *Eridaulus* should be applied. Synonymies of

Hadraule and *Eridaulus* and a redefinition of the latter genus are given below.

HADRAULE Thomson

Hadraule Thomson, 1863, Skand. Col., 5:182; Sahlberg, 1926:71; Lohse, 1964:119. Type, by monotypy, *Cis elongatulus* Gyllenhal, 1827:627.

Cis (*Hadraule*), Seidlitz, 1872:44; Kiesenwetter, 1877:188; Reitter, 1878:24; Seidlitz, 1891:281; Schilsky, 1900:37F (in part); Reitter, 1902:47 (in part); Dalla Torre, 1911:5; Jacobson, 1915:953 (in part).

Pityocis Peyerimhoff, 1918, Bull. Soc. Ent. France, 1918:141. Type, by monotypy, *Pityocis coarctatus* Peyerimhoff, 1918:142 (=*Cis elongatulus* Gyllenhal). [See Peyerimhoff, 1933.]

Ennearthron (*Knablia*) Roubal, 1936, Festschr. 60 Geburtst. Embrik Strand, 1:53. Type, by monotypy, *Cis elongatulus* Gyllenhal, 1827:627.

Hadraula Leng, 1920:246, incorrect subsequent spelling.

ERIDAULUS Thomson

Eridaulus Thomson, 1863, Skand. Col., 5:191; Seidlitz, 1872:45; Sahlberg, 1926:79. Originally included species: *Anobium nitidum* Fabricius, 1792:238 and *Cis jacquemarti* Mellie, 1848:328. Type not designated.

Cis (*Eridaulus*), Kiesenwetter, 1877:191; Reitter, 1878:21, 24; Seidlitz, 1891:281; Schilsky, 1900:37F; Reitter, 1902:48; Dalla Torre, 1911:5; Roubal, 1912:29; Roubal, 1937:39; Chujo, 1940:132; Miyatake, 1954:49; Nakane and Nobuchi, 1955:49; Nobuchi, 1955:56; Nobuchi, 1960b:65.

Xestocis Casey, 1898, Jour. New York Ent. Soc., 6(2):85; Dalla Torre, 1911:20; Dury, 1917:15 (in part); Leng, 1920:247; Hatch, 1962:231. Type, by present designation, *Xestocis levettei* Casey, 1898:85. NEW SYNONYMY.

Anobium, *Ptinus*, *Cis* auctt.

Form oblong, strongly convex; vestiture of short, fine hairs, longer recumbent hairs, or short, stout setae. Head moderately declined, partly covered by pronotum; frontoclypeal ridge of male produced on each side forming 2 flattened plates which are rounded to triangular; genal ridge strongly elevated and carinate, forming relatively deep antennal fossa. Antennae 10-segmented, with a 3-segmented club. Pronotum strongly convex, variously margined laterally, anterior angles rounded to produced and acute; anterior edge in male simple or produced and emarginate. Elytra with dual punctation, consisting of larger nude macropunctures, and smaller setiferous micropunctures, the punctures uniform or seriate. Prosternum relatively short, strongly tumid, concave laterally and carinate mesially; intercoxal process relatively narrow but not laminate, subacute at apex. Protibia expanded at apex, outer apical angle produced and dentate. Sternite III of male with median pubescent fovea or patch.

A large genus with a primarily Holarctic distribution, but extending south at least in the Pacific region. Closely related to *Cis* and *Strigocis*, but distinguished by the strongly carinate prosternum, dual elytral punctation, and produced and dentate protibial apices. The genus differs from *Hadraule*, *Orthocis*, and *Dolichocis* in general body form and by the dentate protibial apices, as well as by the carinate prosternum. Most of the species in this genus feed on the larger woody fungi, such as *Fomes* and *Ganoderma*.

3. *ORTHOCIS*, *MELLIEICIS*, AND *DOLICHOCIS*

Casey (1898) proposed the genus *Orthocis* for the two American species, *Cis punctatus* Mellie and *Orthocis aterrima* Casey, which were distinguished from the species of *Cis* by the ". . . more parallel form of the body . . . glabrous surface, margined elytral suture, and . . . simple apex of the anterior tibiae." Dury (1917) described a third species, *O. longula*, from the eastern U.S. and Kraus (1908) added two species, *O. hucsanus* and *O. pulcher*, from Florida. Another species, *O. platensis* Brèthes (1922), was described from Argentina.

In the European literature, it has long been recognized that *Cis alni* Gyllenhal, and several related forms, such as *C. perrisi* Abeille de Perrin and *C. coluber* Abeille de Perrin, form a distinct group, characterized by the elongate body form, short pubescence, simple protibial apices, and lack of distinct sexual modifications on the head or prothorax of the male. Lohse (1964) proposed for these species the subgenus *Mellieicis* and selected *Cis alni* as its type. Although the exact limits of the subgenus were not given in Lohse's paper, it was indicated that all species of *Cis* with rounded or truncate protibial apices should be included. Having studied the European literature and examined specimens in the American collections, I have come to the conclusion that both *Cis punctatus* Mellie *sensu* Casey and *Orthocis aterrima* Casey are very closely related to the Palearctic species in the *Cis alni* group. The name *Orthocis*, then, should apply to this group of species, and *Mellieicis* should be considered a junior synonym.

In 1908, Kraus described 3 species of *Ennearthron*, *E. annulatum*, *E. transversatum*, and *E. pallidum*, from the southeastern

United States and Cuba, which differ from the species of *Orthocis* only in the possession of 9-segmented antennae. I think it is only sensible to expand the definition of *Orthocis* to include these species as well, instead of leaving them in a genus which appears to be a conglomerate of unrelated forms. If the limits of the group are thus expanded, it becomes necessary to consider several other species which might be included. In 1919, Dury described the genus *Dolichocis* with the single species *D. manitoba* Dury, the main characteristics being the 9-segmented antennae, narrow, cylindrical form, vestiture of short bristles, and rounded protibial apices. The species differs from the American species of *Orthocis*, not only in its antennal segmentation, but by its stouter pubescence, anteriorly constricted prothorax, and the presence of 2 clypeal tubercles and a pubescent fovea on the head of the male. Hatch (1962) described a second species, *D. indistinctus*, from western North America, which is very similar to and obviously congeneric with *Enncarthron laricinum* (Mellie) of the European fauna. Other Palearctic species which might be in the same group are *Enncarthron yuasai* Chujo, *E. pruinosulum* (Perris), and *E. poriae* Nakane and Nobuchi, the last two of which resemble *Orthocis* more than *Dolichocis* in the more quadrate prothorax with broader lateral margins and in the absence of sexual modifications on the head of the male. The problem is made more complex by the presence of 3 Palearctic species, *Cis festivus* (Panzer), *Cis pygmaeus* (Marsham), and *Cis rhododactylus* (Marsham), and one North American species, *Cis angustus* Hatch, which share certain characteristics with both *Cis* and *Orthocis*. Nyholm (1953) noted that the first three all have truncate or rounded protibial apices, and I have observed the same character in *C. angustus*. Yet all of these have sexual ornaments on the head of the male, and they differ in general appearance from typical *Orthocis*. The setting of generic limits, if this is at all justified, presents a difficult problem, which can be solved only after a more detailed investigation of all species involved. In the present discussion, I will make a few suggestions based on a rather superficial study of a large number of forms from various parts of the world and a more intensive study of American representatives.

In the North American fauna, both *Orthocis* and *Dolichocis* seem to be well defined both morphologically and biologically. All of the species of *Orthocis* are elongate and parallel, with a vestiture of very short and fine hairs, a fairly smooth and shining surface, margined elytral suture, flat or slightly tumid prosternum, rounded protibial apices, and an absence of sexual ornaments on the head of the male. There is a tendency in some species (*O. longulus* Dury) towards an extreme attenuation of the body, and several subtropical forms are bicolored and may have 9-segmented antennae. Field observations indicate that at least some species occur under bark, in decaying branches and vines, and apparently not in the tougher fruiting bodies of most Polyporaceae. The genus is more common in the southern part of the continent, and a number of unnamed species have been seen from Central and South America. The two species of *Dolichocis,* on the other hand, differ in having the prothorax constricted anteriorly, the vestiture consisting of short, stouter bristles, and the head modified in the male. Both species occur in the northern part of the continent, and, like most *Eridaulus,* they occur mainly on the fruiting bodies of woody fungi.

In the European fauna, generic distinctions are not so easily made. *Cis coluber* Abeille de Perrin, *C. reflexicollis* Abeille de Perrin, and *C. juglandis* Reitter appear to be closely related to *O. alni,* but they all have a stouter pubescence. Members of the *Cis festivus* group differ both in vestiture and in the presence of clypeal tubercles in the male. Of the species with 9-segmented antennae, *E. laricinum* undoubtedly belongs to *Dolichocis*, but *E. pruinosulum* appears to be closer to *Orthocis*. One character which has been overlooked by most European workers is the margined elytral suture in species of *Orthocis*. At the apex of each elytron, there is a distinct raised margin which curves laterad, leaving a narrow flat area between it and the edge of the suture. I have observed this in *O. alni*, as well as in the American species. This character, in combination with others mentioned above, might serve to distinguish consistently the species of *Orthocis* from those of *Cis* and *Dolichocis*. Several other features which I have observed only in the North American *Orthocis* are the elongate prementum, elongate maxillary stipes with a flattened laterally placed lacinia, and the deeply emarginate, mesially unpigmented, 8th sternite of the male. An investigation of these and other more cryptic characters in the European species may shed some light on their true relationships.

Orthocis, like *Eridaulus*, is so similar to *Cis* that the question arises whether a generic distinction is justified or not. I think that the same criteria can be used here as were applied in the case of *Eridaulus.* The size of the group is quite large, especially in view of the number of unnamed species which I have seen, and the distribution is probably cosmopolitan, with the majority of species occurring in tropical and subtropical regions. Several unique trends occur within the genus, and it appears that the group may have given rise to some of the peculiar endemic forms on the Hawaiian Islands and in other Pacific areas. The latter resemble *Orthocis* in the minute vestiture, flattened prosternum, simple protibial apices, and lack of male ornaments, but they vary considerably in body form, sculpture, and coloration. The trend towards extreme attenuation has already been mentioned.

The biological characteristics of the genus, although briefly mentioned above, deserve further comment. Most of the species of Ciidae feed on the sporophores of wood-rotting fungi, especially the more fibrous or woody fruiting bodies of the Polyporaceae and Hydnaceae. These species have evolved various morphological and physiological adaptations to enable them to cope with a substrate which not only presents a physical barrier to feeding but usually contains little moisture and a high percentage of pure chitin, unavailable to insects not possessing a symbiotic intestinal flora. In addition, there has been a tendency for various species to specialize in certain groups of host fungi (Paviour-Smith, 1960). The species of *Orthocis,* whose habits have been recorded, appear to be general fungus feeders, occurring under bark, in dead branches and vines, in more humid situations, and in association with mycelia and fruiting bodies of a wide variety of wood-rotting fungi. The fungus sporophores are usually of a softer and more ephemeral type and their locations permit a certain amount of bacterial and fungal decomposition, so that the resulting substrate is more easily utilized by the beetles. Benick (1952) has reported *Cis alni* from such diverse fungi as *Exidia glandulosa* (Tremellaceae), *Stereum rugosum* (Thelephoraceae), and *Auricularia auricula-judae* (Auriculariaceae), while Lucas (1849) found the same species (as *C. punctulatus* Lucas, *non* Gyllenhal) on *Schizophyllum commune* (Agaricaecae). Blatchley (1910, 1923) noted that *O. punctatus* was taken by sifting debris from an oak log and that *O. pulcher* was found by beating dead branches of oak. Kraus (1908) bred *Ennearthron transversatum* from decaying rattan vines. Perris (1877) described the larva of *Cis coluber* from dead branches of chestnut and oak in which the fungus

Thelephora was growing; he also noted that the beetle could not be found on branches still remaining on the tree. In the same paper, he noted that the habits of *C. alni* and *C. reflexicollis* Abeille de Perrin were similar, and that *C. oblongus* Mellie and *C. pruinosulus* were taken on fungus-infested elm branches. Zimmerman (1938, 1942) and Swezey (1954) have recorded a number of Pacific island species from dead vines and branches, and those which I have examined seem to fall within this same group.

One fact that makes the study of the particular group more difficult is that most of the shared characters are both simple and apparently primitive. Most of the special modifications which are characteristic of the family as a whole, such as the development of protibial structures for boring (expanded apices, teeth, combs, spines), various prosternal modifications (shortening, carination, reduction of intercoxal process and increased coxal size), presence of sexual ornaments on the head and pronotum of the male, and the development of more complex punctation and vestiture, are all absent in the species of *Orthocis*. In addition, the generalized fungus-feeding habit may be considered primitive. Members of closely related families, such as the Lathridiidae and Corylophidae, share this habit with the species of *Orthocis*, and Crowson (1955) thinks that this may have been characteristic of the ancestral Cucujoidea. If these characters are primitive or plesiomorphic, they are, according to Hennig (1965), less reliable than derivative or apomorphic ones in determining relationships. If, on the other hand, *Orthocis* represents a collection of two or more convergent groups, which have secondarily developed this type of feeding habit and thus have lost, through disuse, the structural modifications associated with boring, this convergence would probably be difficult to detect because of the simplicity of the resulting characters. I favor the hypothesis that these characters are primitive, rather than derivative, and that the feeding habits probably represent those of the common ancestor of the group. In certain other species, such as *Hadraule elongatula* and *Maphoca blaisdelli*, which have similar biologies, this simplified condition also occurs, but other characters indicate that both of these are derivative forms, which may have evolved from a species in the *Cis comptus* group.

I think that most of the species discussed above should be placed in a distinct genus, to which the name *Orthocis* applies. The exact limits of the genus remain uncertain, especially with reference to the inclusion of *Cis festivus* and its relatives, and it is hoped that Dr. Lohse will shed some light on the relationships of these European species. I would definitely exclude *Cis angustus* Hatch, which does have a truncate protibial apex, but which occurs on *Fomes pinicola*, has clypeal tubercles in the male, and lacks a margin on the elytral suture.

The species of *Dolichocis*, although they share certain characters with *Orthocis*, should remain in a separate genus, differing by the absence of the margin on the elytral suture, the anteriorly constricted prothorax, cylindrical form, and vestiture of short, stout setae. The genus should include the species *laricinus* (Mellie), *yuasai* (Chujo), *manitoba* Dury and *indistinctus* Hatch. All four species occur on the larger, woody fruiting bodies of fungi, such as *Fomes pinicola* and *F. officinalis*. Synonymies and redefinitions of *Orthocis* and *Dolichocis* are given below.

ORTHOCIS Casey

Orthocis Casey, 1898, Jour. New York Ent. Soc., 6(2):84; Kraus, 1908:77; Dalla Torre, 1911:20; Dury, 1917:13; Leng, 1920:247; Brèthes, 1922:302. Type, by present designation, *Orthocis aterrima* Casey, 1898:84.

Cis (*Mellicicis*) Lohse, 1964, Ent. Blätter, 60(2):122. Type, by original designation, *Cis alni* Gyllenhal, 1813:386. NEW SYNONYMY.

Ennearthron, Kraus, 1908:78.

Cis (in part), auctt.

Form elongate and somewhat depressed to narrowly elongate and cylindrical; vestiture of very short fine hairs or stouter bristles. Head slightly to moderately declined, only slightly covered by pronotum; frontoclypeal ridge without distinct sexual modifications in male; antennal fossa shallow. Antenna 9- or 10-segmented, with 3- segmented club, segments III and IV usually elongate; maxillary stipes elongate, lacinia lateral, palp relatively stout; prementum elongate. Pronotum subquadrate, sides narrowly margined to broadly margined and explanate, anterior angles truncate to slightly produced and rounded; anterior edge simple in both sexes. Elytra usually parallel sided; punctation single and relatively uniformly distributed; suture margined posteriorly, the margin curved laterad just before apex. Prosternum flat to slightly tumid, longer than intercoxal process which is fairly broad; procoxae subtransverse, narrowly open behind. Protibia only slightly expanded at apex, outer apical angle truncate or rounded. Metasternum slightly convex, the suture moderately long. Sternite III of male with a median pubescent fovea or patch.

A large, widespread genus, but mainly tropicopolitan. Closely related to *Cis* and *Dolichocis*, from which it differs by the rounded protibial apices, margined elytral suture, and lack of distinct sexual ornaments in the male. The species appear to be general fungus feeders, occurring often on dead vines and branches penetrated by fungus mycelia.

DOLICHOCIS Dury

Dolichocis Dury, 1919, Canad. Ent., 51:158; Hatch, 1962:234. Type, by monotypy, *Dolichocis manitoba* Dury, 1919:158.

Cis (in part), Mellie, 1848:236; Lacordaire, 1857:551; Jacquelin Du Val, 1861:237; Seidlitz, 1872:44; Kiesenwetter, 1877:178.

Ennearthron (in part), Abeille de Perrin, 1874:80; Reitter, 1878:30; Seidlitz, 1891:285; Schilsky, 1900:37B; Reitter, 1902:59; Dalla Torre, 1911:23; Chujo, 1941:85.

Form elongate, cylindrical; vestiture of short, stout, suberect bristles or squamae. Head moderately declined, partly covered by pronotum; frontoclypeal ridge of male bituberculate, vertex simple or foveate; antennal fossa shallow. Antenna 9-segmented, with 3-segmented club; maxillary stipes subquadrate, lacinia subterminal, palp relatively stout. Pronotum almost as long as wide, somewhat constricted anteriorly, sides narrowly margined, anterior angles not or barely produced; anterior edge simple in both sexes. Elytra elongate and subparallel; punctation single and fairly uniformly distributed. Prosternum slightly tumid, slightly longer than intercoxal process which is fairly broad and blunt at apex; procoxae subtransverse, narrowly open behind. Protibia only slightly expanded at apex, outer apical angle truncate or rounded. Metasternum slightly convex, suture moderately long. Sternite III of male with a median pubescent fovea.

A small genus restricted to the Holarctic region. Closely related to *Cis* and *Orthocis*, from which it differs in the rounded protibial apices, stout vestiture, constricted prothorax, and lack of a margin along the elytral suture. The 4 species all occur on *Fomes pinicola* and related fungi.

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THE FOSSIL ELEPHANT SHREWS (FAMILY MACROSCELIDIDAE)

By Bryan Patterson

With One Plate

CAMBRIDGE, MASS., U.S.A.
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No. 6 — *The Fossil Elephant Shrews (Family Macroscelididae)*

By Bryan Patterson

INTRODUCTION

The history of this peculiar group of mammals was ostensibly a blank until 1937, when Broom described an extinct species of *Elephantulus* from the Pleistocene of South Africa. Four extinct genera, however, had been described earlier, from 1910 on, but, having been placed incorrectly in other groups of mammals, had gone unrecognized. One of these, *Palaeothentoides* Stromer, has been detected as a macroscelidid by Butler and Hopwood (1957); the other three, *Metoldobotes* Schlosser, *Myohyrax* Andrews and *Protypotheroides* Stromer are here placed in the family for the first time. *Palaeothentoides* was originally described as a marsupial, *Metoldobotes* as a mixodectid insectivore, and *Myohyrax* and *Protypotheroides* as hyracoids. So extraordinary a situation is, I believe, without parallel in mammalian paleontology.

This paper came into being in a rather roundabout way. Creatures with names such as *Palaeothentoides* and *Protypotheroides* have a certain fascination for anyone with a taste for South American fossil mammals. Being in Europe during the spring of 1957, I took the opportunity of visiting Munich and examining material of both forms. The collection included an important undescribed specimen of *Palaeothentoides africanus*, and this I was very kindly permitted to borrow for further study. Shortly after completing the description of it, and with the details of macroscelidid dental structure fresh in mind, I had occasion to consult Schlosser's memoir (1911) on Fayum mammals during a discussion of the dental formula of *Parapithecus*. There, staring up from the plate, was *Metoldobotes*, an obvious macroscelidid. (Discussions of *Parapithecus* are perennial; it is gratifying to be able to report this useful by-product of one of them.) On examining *Protypotheroides beetzi* in Munich I had noted a decided resemblance to *Palaeothentoides*, but at the time had considered it to be an interesting example of convergence, one about on a par with the resemblance to the interatherid typotheres. It was only after consulting Whitworth's study (1954) of the Miocene hyracoids of Kenya in quite another connection that I began to suspect the Myohyracinae really were macroscelidids, a suspicion that hardened to conviction upon examination of Stromer's figures (1926) of postcranial remains from the Miocene of Southwest Africa. Here was a group of elephant shrews that had masqueraded as ungulates for half a century. Broom's (1948) *Mylomygale spiersi* from the Pleistocene, a form with hypsodont, rodent-like cheek teeth, revealed the former existence of yet another phylum of the family. It became clear that the surviving forms give little hint of a rather remarkable radiation that went on within the African continent throughout much of the Cenozoic. There is nothing remotely primate-like about the extinct phyla so far known. The fossil record in fact very definitely supports those who have been unable to accept the hypothesis of a close relationship between the elephant shrews and the treeshrews. As LeGros Clark has well put it (1959, pp. 318–319n): "In retrospect it is difficult to understand this taxonomic association . . . the differences . . . are so marked as to make it clear that they are really quite divergent types."

This study has been aided by National Science Foundation Grants G-3120 and GP 1188, which made it possible for me to examine specimens in Europe and in Kenya. For access to material I am indebted to the authorities of the British Museum (Natural History) and of The American Museum of Natural History, to Dr. Richard Dehm and to Dr. L. S. B. Leakey. Miss Margo Hayes has assembled the final manuscript and assisted in checking localities and references. The photographs are by Mr. Frank White and the drawings by Mrs. Dorothy Marsh. Figures of fossil macroscelidids are widely scattered in the literature and a number of them are in rather rare publications. Those pertinent to the work are accordingly redrawn here. Publication has been aided by National Science Foundation Grant GB-500.

TAXONOMY AND MORPHOLOGY

MACROSCELIDIDAE

MACROSCELIDINAE

METOLDOBOTES Schlosser

Metoldobotes Schlosser, 1910, p. 507; Matthew, 1910, p. 702.
Metolbodotes Schlosser, 1911, p. 70; Matthew, 1915, p. 467.

Type species: M. stromeri Schlosser, 1910.

Distribution: Early Oligocene, north Africa.

Emended diagnosis: I_3 (?), C, P_4, M_2. I_3 not bifid, with pronounced vertical groove on lingual side; C bluntly pointed, three sided; P_{1-3} short relative to $P_4 - M_2$; P_1 single rooted, roots of P_2 very closely appressed, P_3 with small anterior and posterior cusps, without posterior accessory cusp; P_4 and lower M with crista obliqua running to posterior face of trigonid, talonid of M_3 short relative to trigonid. Horizontal ramus of mandible relatively short, deep; ascending ramus steep; symphysis long, extending to P_3.

METOLDOBOTES STROMERI Schlosser

(Fig. 1 c, d)

Metoldobotes stromeri Schlosser, 1910, p. 507; Matthew, 1910, p. 702.
Metolbodotes stromeri Schlosser, 1911, pp. 70–72, 147, 157, 163, 164; pl. 9, fig. 5.

Type: An incomplete right horizontal ramus in the Stuttgart collections, with I_3, C, $P_3 - M_2$, alveoli for I_2, P_1, roots of P_2.

Hypodigm: Type only.

Horizon and locality: Fluviomarine series, early Oligocene; Fayum, Egypt.

Diagnosis: As for the genus. The fragmentary type specimen appears to represent an animal somewhat larger than *Rhynchocyon petersi* and *Protypotheroides beetzi*, and hence the largest known member of the family.

Discussion: Metoldobotes, with the exception of brief comments by Matthew and passing mentions in various editions of Zittel, has remained essentially unnoticed in the literature since its description. Schlosser tentatively assigned it to the Mixodectidae, a reference which, as Matthew (1915, p. 467) stressed, had nothing to recommend it in the way of positive resemblances between the Fayum form and any mixodectid.

The type ramus, incomplete anteriorly, preserves, in series, an anterior alveolus, an incisor, a partially erupted, conical tooth, the alveolus of a single-rooted tooth, the very closely appressed roots of a double-rooted tooth and the last four cheek teeth. Schlosser interpreted this array as $I_{1,2,3}$, C, $P_{3,4}$, $M_{1,2,3}$, but he made no comparisons with any macroscelidid. Inspection of his figures at once reveals an impressive number of resemblances to the various members of this family, and suggests that the dental formula is in reality $I_{(1),2,3}$, C, $P_{1,2,3,4}$, $M_{1,2}$, as in *Rhynchocyon*, *Petrodromus*, *Elephantulus*, *Macroscelides*, and *Mylomygale* (an alveolus for I_1 in this interpretation is lacking, but the specimen is incomplete anteriorly). In the ensuing remarks the teeth will be so designated.

The crown of I_3 is described by Schlosser as being about half the height of the root; this is true of the incisors of macroscelidines. A groove is present on the lingual faces of the incisors of members of this subfamily, although in no case is it as pronounced as shown in Schlosser's figure. The canine in *Rhynchocyon* is sometimes (e.g. MCZ 38782), although by no means invariably, not fully erupted until after the posterior cheek teeth have come into wear. P_1 is single-rooted in *Macroscelides, Mylomygale*, and in some species of *Elephantulus*[1]. The roots of P_2 are closely appressed in *Macroscelides*. P_3 of *Metoldobotes* resembles that of all members of

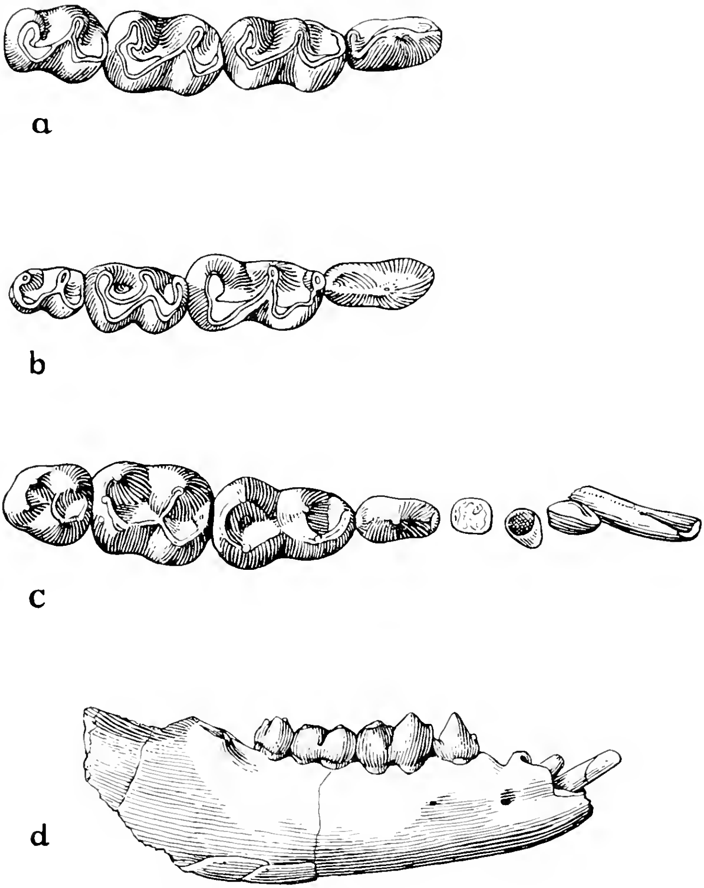

Figure 1. *c, d, Metoldobotes stromeri*, crown view of dentition and lateral view of mandible, *c* $\times 3$, *d* $\times\frac{3}{2}$; redrawn from Schlosser. *a, Petrodromus nigriseta*, MCZ 22434, *b, Rhynchocyon petersi*, MCZ 22573, crown views of $P_3 - M_2$, not to scale.

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[1] Among the *Elephantulus* material in the Museum of Comparative Zoology collections I have found P_1 to be single rooted in *E. ocularis* (29 specimens), *rufescens* (6), and *pulcher* (6); variable in *rupestris* (3 single and 3 double); and double rooted in *intufi* (5), and *fuscipes* (2).

the family in its proportions relative to $P_4 - M_2$ and in its possession of low anterior and posterior cusps, and that of the macroscelidines in the absence of an accessory cusp on the posterior slope of the protoconid. The large P_4 has a wide molariform talonid and a narrower, elongate trigonid. The tooth is typically macroscelidid in these features, and also as regards size relative to the molars and the structure and arrangement of the cusps and crests. The molars of *Metoldobotes* resemble those of the living macroscelidids in the nearly equal heights of the trigonids and talonids, the metaconids and entoconids higher than the protoconids and hypoconid, the absence of labial and lingual cingula and the structure and positions of cusps and crests generally. The paraconid is median, as in the macroscelidines. The crista obliqua runs to the center of the posterior face of the trigonid, as in the Miocene *Rhynchocyon clarki* (Butler and Hopwood, 1957, p. 10), rather than to the metaconid, as is the case in living forms. The relative lengths of M_1 and M_2 are approximately as in *Rhynchocyon*, and the talonid of M_2 appears to be about as small and short relative to the trigonid as in *R. cirnei* (e.g. MCZ 43735). In agreement with *Rhynchocyon* and the macroscelidines, the mental foramina are beneath P_{1-2} and P_4; the ascending ramus, to judge from Schlosser's figure, arises abruptly well behind the last molar. The masseteric fossa is shallow and, as in macroscelidines, extends down to the level of the tooth row. The horizontal ramus is deeper than in either the Rhynchocyoninae or the Macroscelidinae, shallower than in the hypsodont Myohyracinae. That part of the tooth row anterior to P_4 is somewhat shorter relative to the length of the series as a whole than in living members of either of the first two subfamilies, but is approximately comparable to *Myohyrax* and *Mylomygale* in this respect. The symphysis, *fide* Schlosser, extends to P_3 (his P_4) and is hence longer than in all other known members of the family, in which it terminates beneath C or P_1.

On the evidence available it is difficult to assign *Metoldobotes* to subfamily with any confidence. The Fayum form does not, even incipiently, display any of the specializations of myohyracines or mylomygalines. It does resemble both the Rhynchocyoninae and the Macroscelidinae, agreeing with one or the other now in this character, now in that, and differing from both of them in the long symphysis. Resemblances to *Rhynchocyon* — and differences from the macroscelidines — are the small size of the talonid of M_2 relative to the trigonid and the small size of M_2 as a whole relative to M_1. *M. stromeri* resembles the Miocene *R. clarki* in that the crista obliqua runs only to the posterior face of the trigonid and not to the apex of the metaconid, but this is interpretable simply as a primitive character possessed in common. Resemblances to the Macroscelidinae, or at least to some of them, are the lack of a posterior accessory cusp on P_3, the small single-rooted P_1, the closely appressed roots of P_2, the median position of the paraconid in the molars, the lingual groove of the incisor, and the steeply rising ascending ramus. In sum, the characters suggest relationship with the macroscelidines rather than with the rhynchocyonines, and I very tentatively place *Metoldobotes* in the Macroscelidinae.

PALAEOTHENTOIDES Stromer

Palaeothentoides Stromer, 1932, p. 185.

Type species: P. africanus Stromer, 1932.

Distribution: Early Pleistocene?, southwest Africa.

Emended diagnosis: Lower postcanine formula P_4, M_3; P_1 two-rooted, not incisiform; P_{2-3} with anterior cusps little separated from protoconids, P_3 without metaconid and entoconid rudiments; P_4 narrow, metaconid decidedly posterointernal to protoconid, reëntrant valley between metaconid and entoconid nearly filled by swelling on crest running anteroexternally from entoconid, paraconid crest high, anterointernal swelling partially obliterating cleft between anterior crest and metaconid; M_{1-2} with very slight, shallow clefts between paraconids and metaconids, sides of deep reëntrants between metaconids and entoconids parallel, not ventrally converging; horizontal ramus of nearly even depth beneath cheek teeth, slightly downcurving anteriorly.

PALAEOTHENTOIDES AFRICANUS Stromer

(Fig. 2; Pl. 1)

Palaeothentoides africanus Stromer, 1932, pp. 178–185, figs. 1a–2b; Butler and Hopwood, 1957, p. 11.

Type: München No. 1931. VII. 1a, left ramus with $P_3 - M_2$, alveoli for P_{1-2}, M_3.

Hypodigm: Type, and München Nos. 1931. VII. 1b, fragment of left ramus with M_{2-3} (now lost), and 1932. I. 501, left ramus with $P_1 - M_3$.

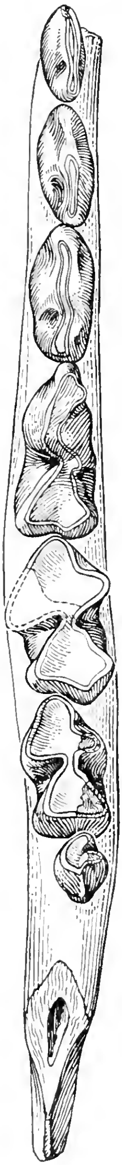
Horizon: The "intermediate terrace" of Wagner and Merensky (1929, p. 29, fig. 5); age uncertain, possibly early Pleistocene. Stromer (1931, p. 41; 1932, p. 185) considered this to be "wohl Mittelpliocän," which would now, with the transfer of the Villafranchian to the Pleistocene, be regarded as late Pliocene. The two other forms definitely identified by Stromer from this level, *Enhydriodon* and *Hyaena* (especially the latter), are not inconsistent with a Pleistocene age.

Locality: Klein Zee (or Kleinsee), near the mouth of the Buffels River on the coast of Little Namaqualand, some 25 miles SSE of Port Nolloth, Union of South Africa.

Diagnosis: As for the genus. Comparable in size to the smaller living macroscelidines.

Description: The first premolar is a long, narrow, double-rooted tooth with a simple crown consisting of a procumbent protoconid, which extends forward beyond the anterior root, connected by a crest to a smaller posterior cusp. The lingual face of the tooth is very slightly convex, the labial vertically grooved between the cusps. P_2 bears a small cusp on the anterior slope of the erect protoconid; labial and lingual grooves are present anterior to the protoconid, and the labial groove between protoconid and posterior cusp is much larger and deeper than in P_1. All these features are accentuated in P_3: the anterior cusp is larger, the grooves deeper, and the posterior cusp larger and wider; there is no metaconid or entoconid rudiment. These three teeth progressively increase in length and height. P_{1-3} of *Palaeothentoides* are very similar to the corresponding teeth of *Nasilio*, differing from those of the other living genera in various particulars. Thus, in *Macroscelides*, P_1 is single-rooted and similar in structure to $I_2 - C$, while P_{2-3} are higher crowned relative to length; in *Elephantulus*, P_1 has a higher protoconid, P_{2-3} have the anterior cusps well separated from the protoconid, P_3 has metaconid and entoconid rudiments, and a rudiment of the metaconid is occasionally seen on P_2; in *Petrodromus* and *Rhynchocyon*, all three teeth are higher, more piercing (especially the caniniform P_1 of the latter), anterior cusps are either lacking entirely (*Rhynchocyon*) or rudimentary (*Petrodromus*), while the posterior cusps are very small in both and, in *Rhynchocyon*, confined to P_3.

P_4, the longest of the cheek teeth, is submolariform, the talonid completely as in M_{1-2}, the narrow trigonid not. The entoconid is fully as large as in the molars and, as in them, higher than the hypoconid. In the trigonid, the anterior cusp is set off labially from the protoconid by a vertical groove wider and shallower than the corresponding ones on the anterior premolars. The groove between these two cusps on the lingual side is shallow and partially filled by a buttress on the side of the ridge connecting them. The metaconid is well developed, nearly as high as the protoconid and decidedly posterointernal to it in position; the short crest between the cusps bears a small, shallow groove on its lingual side. The



crista obliqua runs to the apex of the metaconid. The labial reëntrant between trigonid and talonid is fully as large and deep as in M_{1-2}, but the lingual is to a great extent filled by a vertical swelling on the side of the ridge running from the entoconid to the crista obliqua. The sides of this lingual reëntrant are nearly parallel for most of their heights and converge to form a U only near the base of the enamel. The tooth continues the progressive increase in crown height seen in P_{1-3}. Although thoroughly macroscelidid in structure, P_4 is the most distinctive tooth of the series. None of the living forms has the labial reëntrant between trigonid and talonid nearly filled by a swelling, and in none is the metaconid so far posterointernal to the protoconid. In all except *Macroscelides* the anterior crest and the metaconid are widely separated by a deep groove and the sides of the lingual reëntrant converge toward the base, forming a V.

M_{1-2} consist essentially of two triangular prismatic columns connected by the narrow isthmus formed by the crista obliqua. The protoconids, hypoconids and paraconids are angulate, the metaconids and entoconids more rounded. The paraconids and metaconids are separated by very shallow vertical grooves. The lingual and labial reëntrants are large, deep, and extend nearly to the base of the enamel; their sides are parallel and U-shaped below. The trigonids are wider and larger than the talonids, particularly on M_1. The metaconids and entoconids are higher than the protoconids and hypoconids, and there is a slight indication of a hypoconulid. This cusp may have been larger on the unworn crown, if we may judge from *Macroscelides* in which it is very prominent on unerupted molars but rapidly becomes worn away. On the lingual sides of the crests running forward from the entoconids are faint vertical swellings corresponding to the

Figure 2. *Palaeothentoides africanus*, dorsal view of mandible, München No. 1932. I. 501. ×8.

prominent one in P_4. These molars are the highest crowned of the cheek tooth series. M_3 is vestigial and much lower crowned than M_2. It is composed of the trigonid only, on which the small metaconid is the highest element and the protoconid is subordinated in the paraconid crest; metaconid and paraconid are separated lingually by a shallow depression, and there is a slight vertical ridge on the posterior face, the last vestige of the talonid. The enamel is continuous on all cheek teeth; it is thick on $P_4 - M_2$ although thinning at the paraconids in the molars. M_3 is indistinguishable from that of *Nasilio.* M_{1-2}, on the contrary, are quite different from those of this form and very close indeed to those of *Macroscelides,* differing only in their slightly lower crowns and, at a corresponding stage of wear, in the presence of enamel around the paraconids. In the other living forms, M_{1-2} are somewhat lower crowned, have wide lingual grooves between the paraconids and metaconids, and V-shaped sides to the lingualr eëntrants separating trigonids and talonids.

Seen from above, the ramus curves very slightly inward from P_2 forward and gently outward from M_3 backward. There is no trace of the symphysis on the part preserved, indicating that, as in all living macroscelidids except *Petrodromus,* this did not extend posteriorly beyond the level of the canines. The inner face, as noted by Stromer, is nearly flat, the outer swells out gently opposite the molars. As in other forms, there is a posterior mental foramen beneath P_4 and an anterior beneath P_1. The height of the horizontal ramus remains rather constant beneath the cheek teeth, decreasing less anteriorly than in the living forms. The ventral border is gently convex beneath the molars and P_4, and shows a more marked tendency to turn down beneath P_{1-2} than in any other form. As is usual in the group, the ascending ramus begins to rise well behind the last molar and the masseteric fossa is shallow and poorly defined.

Discussion: Palaeothentoides is unquestionably a valid genus. It resembles *Nasilio* and *Macroscelides,* combining characters of both, and can be referred with assurance to the Macroscelidinae. There is no need to belabor the fact that this form is no marsupial. A resemblance does exist, particularly in the trigonid, between P_4 of *Palaeothentoides* and M_1 of *Palaeothentes,* but this is far from exact. The labial and lingual reëntrants separating trigonid and talonid that are large and deep in the African form are, for example, shallow in the South American one, and in any event the teeth Stromer compared are not homologous.

Stromer himself realized almost at once that *Palaeothentoides* was not a marsupial. A separate of his paper in my possession bears a typewritten slip reading: "*Berichtigung:* Durch einen neuen Fund ist erwiesen, dass Palaeothentoides 4 Pm and 3 M hat, also sicher kein Didelphier ist." So far as I am aware, however, he never published this retraction. The "new find" referred to is of course No. 1932. I. 501, here described and figured for the first time.

Measurements, in mm, of München No. 1932. I. 501.

	P_1	P_2	P_3	P_4	M_1	M_2	M_3
Length	1.4	2.0	2.3	2.8	2.4	2.1	0.8
Width	0.6	0.7	0.9	1.4	1.7	1.5	0.8

Length $P_1 - M_3$, 14.0; P_{1-4}, 8.6; M_{1-3}, 5.6.
Height of ramus beneath M_1, external, 2.9.

ELEPHANTULUS Thomas and Schwann

Elephantulus Thomas and Schwann, 1906, p. 577.
Elephantomys Broom, 1937, p. 758.

In the course of describing the Pleistocene *E. langi*, Broom observed that certain species of the genus, *langi* among them, have a molariform P^2. Believing that *E. rupestris*, the type species, lacked this character, he proposed *Elephantomys*, with *E. langi* as type, for the reception of those species possessing it. Shortly thereafter, specimens from what he supposed to be the type locality of *E. rupestris* having come to hand, he concluded that this species did after all have a molariform P^2, a fact which in his opinion effectively suppressed *Elephantomys*. He did not go on to erect a new genus for those forms with a non-molariform P^2.

Elephantomys was subsequently revived by Ellerman, Morrison-Scott and Hayman (1953, p. 8). Stating that P^2 of the type of *E. rupestris* was non-molariform, they recognized *Elephantomys* as a subgenus, distinguishing it on the basis of the molariform P^2 and the possession of less flattened bullae, in which the lateral (i.e. tympanic) portion is higher relative to the median (i.e. entotympanic) than in *Elephantulus*[1]. These distinctions are not valid. As regards P^2, what is involved is a forward extension of the molarisation field. In *Rhynchocyon* and *Petrodromus* this extends hardly or not at all beyond P^4; in *Nasilio* and *Macroscelides* P^{2-3} have been incorporated to the degree that two lingual cusps are

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[1] They also reduced *Nasilio* to the rank of a subgenus of *Elephantulus*. This does not seem justified. In addition to possessing M_3, *Nasilio* has higher-crowned posterior cheek teeth and different hind limb proportions (Evans, 1942).

present on them. *Elephantulus* is in a state of flux. Among the material available to me, P^2 is molariform in *intufi* (5 specimens) and *fuscipes* (2), non-molariform in *rupestris* (5) and *pulcher* (7). Although predominantly non-molariform in *ocularis* (29) and *rufescens* (6), it is nevertheless variable in these species, even within what are surely local populations. Thus, in *rufescens* from Mt. Mbololo, Kenya, of two specimens collected on the same day, one (MCZ 31800) has two lingual cusps on P^2, another (MCZ 31802) one. Within *ocularis*, a small series from Unyanganyi, Tanganyika, Tanzania, includes two specimens (MCZ 25660 and 25683) with two lingual cusps on this tooth and three with one; a specimen from Dodoma, Tanganyika (MCZ 22841), has two lingual cusps on the left side and one on the right. Within the "non-molariform" species, P^3 as well as P^2 is variable in respect of lingual cusp development. A distinction based on bulla structure cuts across one based on premolar structure. Thus the "non-molariform" *pulcher* has a "flattened" bulla, and the predominantly "non-molariform" *rufescens* and *ocularis* have "less flattened" ones. *Elephantomys* does not merit recognition.

A far reaching proposal for a division of *Elephantulus,* and indeed of the whole subfamily, has been advocated by Van der Horst, who, with co-workers, devoted many years to study of the embryology of the genus, with particular reference to *E. myurus jamesoni* (I employ Van der Horst's names in this paragraph). In the course of his work there emerged the remarkable facts that in this form approximately sixty eggs are liberated and approximately sixty corpora lutea develop in each ovary, only one of which becomes implanted, the Graafian follicle is remarkably small, and fat globules are lacking in the ova. *Macroscelides proboscideus* was found to agree in all these particulars, and *E. capensis* in all save for the presence of a few fat globules. *E. intufi* and *E. rupestris* stand in striking contrast. In these species only two eggs per ovary are liberated, the Graafian follicle is of normal type, and fat globules are present. *Petrodromus tetradactylus* is in agreement with them except for the apparent absence of fat globules. On the basis of all this, Van der Horst has suggested (e.g. 1944) that there are only two genera of macroscelidines and that the division passes through the genus *Elephantulus* of current usage. He has not spelled out what would result were his suggestion to be adopted, but this can be simply put. We would have two genera: *Macroscelides,* with *proboscideus, myurus* and *capensis,* and *Petrodromus,* with *tetradactylus, rupestris* and *intufi*; all other species would have to remain in limbo until comparable investigations had been carried out on them. If these characters were indeed the touchstone of macroscelidine systematics such a situation would be acceptable, but there is no real evidence that they are. The genera recognized by mammalogists over the years are clear-cut taxa, distinguishable by different combinations of characters. The sporadic occurrence of the curious ovarian characters suggests that these were independently acquired, or, alternatively, perhaps lost, at various times within the group.

This possibility is reënforced if the classification, other than subgeneric, of the South African species and subspecies of *Elephantulus* proposed by Ellerman, Morrison-Scott and Hayman is correct. Van der Horst's *myurus jamesoni* is their *rupestris jamesoni*, his *capensis* is their *rupestris capensis*, his *intufi* and *rupestris* may be their *rupestris* and *intufi*. His division of the subfamily would thus run between subspecies of *rupestris* in their arrangement. The genetic basis of the ovarian peculiarities may be of a rather simple sort.

ELEPHANTULUS LANGI (Broom)

Elephantomys langi Broom, 1937, pp. 758–760, fig. 5.
Elephantulus langi Broom, 1938, p. 251; 1948, p. 5.

Horizon: Pleistocene.

Locality: Cave deposit at Schurveberg, 15 miles west of Pretoria, Transvaal, Union of South Africa.

E. langi is evidently represented by rather rich material from the Schurveberg cave deposit, and Broom's description is of the most preliminary sort. The relationship between *langi* and living forms remains to be determined.

ELEPHANTULUS ANTIQUUS Broom

Elephantulus antiquus Broom, 1948, pp. 5–6, fig. 3.

Horizon: Earlier Pleistocene.

Locality: Bolt's workings, Sterkfontein, Transvaal, Union of South Africa.

E. antiquus is evidently distinct from *E. langi* — it has, e.g., a non-molariform P^2 — but little more can be said. As in the case of *E. langi*, there is fairly abundant material, Broom's description is preliminary and incomplete, and the relationship to living species is unknown. In 1946, Broom (*in* Broom and Schepers, p. 78) stated that: "The elephant shrew *Elephantulus langi*, or one very closely allied, occurs in the Plesianthropus cave. The type is from Schurveberg, Pretoria. It is common at Bolt's workings." Presumably the species there referred to is *E. antiquus*.

ELEPHANTULUS ROZETI (Duvernoy)

From an archaeological site at Redeyef, Tunisia, Gobert (1912) recorded the presence of various genera of mammals, most of which he believed to be referable to living species. *Macrocelides* (*sic*) is among those listed. Three cultural levels occur at the site, the two lower Paleolithic and the upper ranging from transitional to Neolithic. Gobert gave no description of the mammalian remains, which it would appear from the text were found in the upper level. Romer (1928, pp. 100, 153, 161) lists this find as *Macroscelides rozeti*. A little uncertainty attaches to the determination. Thomas (1901, 1913) split North African *Elephantulus* into two species, *E. rozeti* and *E. deserti*, the former with three and the latter with two subspecies. *E. deserti* is the more eastern of the two and, if valid, the Redeyef material might therefore be referable to it. More likely than not, however, subspecific distinction, at most, is involved. Although Thomas had stated, in 1901, that *deserti* did not differ in size from *rozeti*, he claimed, in 1913, that it was smaller; the very few published measurements do not support the assertion. The differences appear to be confined to pelage color.

Elephantulus rozeti, which dates from 1838, was long known as *Macroscelides rozeti*, and numerous specimens so labeled found their way into collections. Many of the labels were not changed when Thomas and Schwann transferred *rozeti* to their new genus *Elephantulus*. These labels have trapped trusting anatomists and paleontologists. A number of accounts and illustrations in the literature that purport to be of *Macroscelides* are actually of *Elephantulus*, based on *E. rozeti* (e.g. Evans 1942, Fiedler 1953, Grassé 1955, Saban 1956–1957, Van der Klaauw 1929, in part).

RHYNCHOCYONINAE

RHYNCHOCYON Peters

RHYNCHOCYON CLARKI Butler and Hopwood

R. clarki Butler and Hopwood, 1957, pp. 4–11, figs. 2–3.

Horizon: Early Miocene.

Localities: Type from Songhor local fauna, Kenya; referred material from Rusinga Island, Kenya, found in the upper and lower Hiwegi beds and either in the Kiahera or in the lower part of the Kathwanga beds.

This species, so well described by its authors, reveals, as they point out, that the two surviving subfamilies had diverged prior to the Miocene. *R. clarki* ". . . as an early member of the *Rhynchocyon* lineage . . . is . . . nearer to the common ancestor of the two groups, and possesses a number of primitive characters which have been lost in Recent representatives of both subfamilies." The species is notably smaller than the living members of the genus, which suggests a relatively recent increase in size within the *Rhynchocyon* lineage.

MYLOMYGALINAE subfam. nov.

Diagnosis: I_3, C, P_4, M_2. I_{1-3} small, subequal; C $-$ P_2 small, single rooted; P_4 $-$ M_2 large, hypsodont, crowns complex, flat, of grinding type. Molars compressed anteroposteriorly, as wide as long; protoconid and hypoconid angulate, directed antero-externally; hypoconid and hypoconulid forming posterior lophid, entoconid set off from posterior lophid by deep reëntrant; reëntrant between paraconid and metaconid situated on anterior face of tooth; M_2 large relative to M_1. Talonid of P_4 fully molariform, trigonid larger, more elongate than in molars. Ventral border of horizontal ramus strongly convex, alveolar border concave beneath posterior cheek teeth.

MYLOMYGALE Broom

Mylomygale Broom, 1948, p. 6.

Type species: M. spiersi Broom.

Distribution: Earlier Pleistocene, south Africa.

Diagnosis: Sole known genus of the subfamily diagnosed above.

MYLOMYGALE SPIERSI Broom

(Fig. 3)

Mylomygale spiersi Broom, 1948, pp. 6–8, fig. 4, (1946, *in* Broom and Schepers, p. 28, fig. 1 N–O[1]).

Locality: ". . . a small cave about half a mile to the north of the cave which yielded the Taungs man-ape skull." Approximately 80 miles N. of Kimberly, Bechuanaland, Union of South Africa.

Horizon: Earlier Pleistocene. ("This bone breccia is probably of approximately the same age as [those in] the other caves.")

Diagnosis: Sole known species of the genus.

Discussion: This remarkable little macroscelidid enjoys the distinction of being the only extinct genus correctly placed in the

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[1] In this paper *M. spiersi* was figured and listed with the statement that: "It represents a new family of the Menotyphla." No diagnosis or description was given.

family by its describer. Discovery of *Mylomygale* revealed the existence of an otherwise unknown division of the family, one that evolved posterior cheek teeth that are as strikingly rodent-like as those of the myohyracines are ungulate-like. Broom's remark to the effect that had the molars been found isolated they would have been regarded as belonging to some peculiar hystricomorph rodent is no exaggeration.

The type specimen preserves five small alveoli followed by four grinding teeth. Although he decided that the dental formula was probably I_3, C, P_4, M_2, Broom was in some doubt as to whether the last two alveoli housed the roots of two teeth or of one. "As in all the living Macroscelids the anterior premolars are double-rooted it might seem more probable that the two sockets held a single premolar, but on the other hand if the anterior premolar were double-rooted then there can only be three premolars, while all living Macroscelids have four. . . . I think it more likely that there were two small single-rooted premolars." This tentative conclusion was, I believe, the correct one. Contrary to Broom's statement, and as pointed out above, the roots of P_1 are fused in *Macroscelides*, in some species of *Elephantulus*, and in the extinct *Metoldobotes*, while the roots of P_2 are closely appressed in *Macroscelides*. The anterior portion of the horizontal ramus is short in *Mylomygale*, and it is hence not surprising that the roots of P_2 had fused.

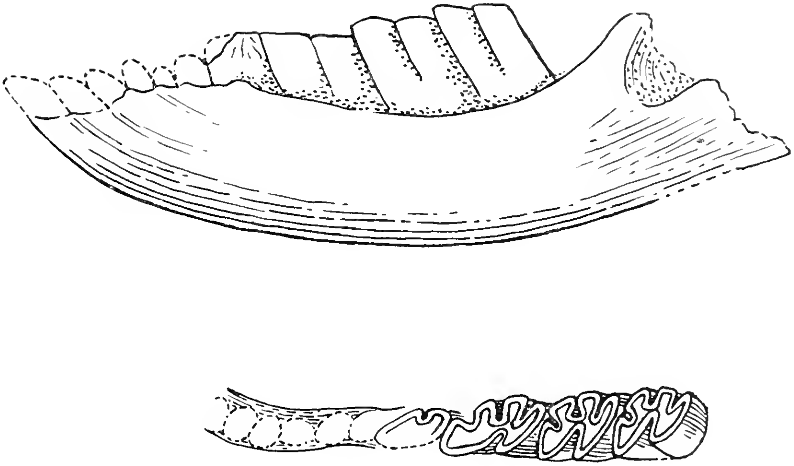

Figure 3. *Mylomygale spiersi*, lateral view of mandible and crown view of dentition, ×4; redrawn from Broom.

P_3, the most anterior tooth preserved, bears the same size relation to P_4, and P_4 to the molars, as in other members of the family. P_4 and the two molars are remarkable for their deep, narrow, and persistent reëntrant folds. Comparison with an unworn molar of *Macroscelides* (Fig. 5h) permits an understanding of the cusp pattern. The anteroexternal angle is composed of the protoconid and the centrally situated paraconid. Hypoconid and hypoconulid are joined to form the posteroexternal and posterointernal angles and the posterior lophid. The metaconid makes up the anterointernal angle and the entoconid the central internal. This degree of independence of the entoconid is a departure from the usual macroscelidid condition, in which entoconid and hypoconulid tend to be connected (cf. Fig. 1a, b). The large size of M_2 relative to M_1 is another character peculiar to *Mylomygale* within the family; in all other known genera, even in the earliest, *Metoldobotes*, it is decidedly smaller than its predecessor in the series. The size of this tooth provides an example of the reversal of an evolutionary trend, the reversal in this case being associated with the later trend toward the acquisition of rodent-like posterior cheek teeth.

MYOHYRACINAE

(= Myohyracidae Andrews 1914, Myohyracoidea Stromer 1926)

(Figs. 4b; 5a, b, c, f, i, j; 6a, c, e, g, i)

Emended diagnosis: Macroscelididae with complete dental formula; I^{1-2}_{1-2} large, without enamel on lingual faces; posterior cheek teeth hypsodont; M^3_3 greatly reduced; P^{2-3}_{3} submolariform, P^4_4 essentially molariform; $P^3 - M^2$ with moderately undulant ectoloph, paracones and metacones with comparatively shallow labial grooves between them, parastyles and metastyles prominent, parastyles anteroexternal in $P^4 - M^2$; $P^2 - M^2$ with persisting fossettes, those of molars arranged in anterior and posterior pairs; $P_3 - M_2$ with two fossettids, one each in trigonid and talonid; horizontal ramus deep beneath posterior cheek teeth, mental foramen beneath P_3.

Distribution: Early Miocene, east and southwest Africa.

Genera included: Myohyrax Andrews 1914, *Protypotheroides* Stromer 1922.

Discussion: Andrews (1914, pp. 169–171) described *Myohyrax oswaldi* on a fragment of a ramus with $P_3 - M_2$ and some isolated teeth, including an upper molar; this material gave no hint of the vestigial nature of M^3_3. With such evidence in hand it would hardly occur to anyone to make a comparison with the macroscelidids, and Andrews did not do so. He referred the genus to a new family of the Hyracoidea. All subsequent students have looked at myohyracines in this light and some of them have commented on how aberrant they are within that order. From the work of Stromer (1926) and of Whitworth (1954), it is possible to note that many of the characters in which they differ widely from hyracoids are actually points of resemblance to macroscelidids.

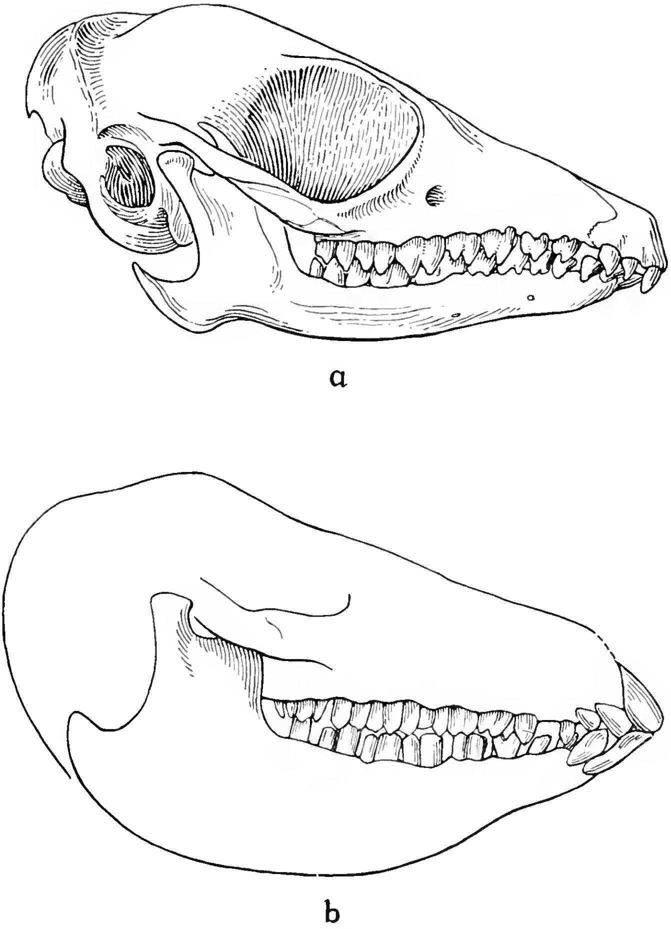

Figure 4. Lateral views of skull and mandible of, *a*, *Nasilio brachyrhynchus*, MCZ 43755, and, *b*, *Myohyrax oswaldi*, slightly modified from Whitworth; *b* ×2, *a* not to scale.

The skull of *Myohyrax*, figured in outline by Whitworth, is not dissimilar to those of other members of the family (Fig. 4). The facial region in all is long, low and rather narrow; the cranium is short and high; the zygoma arises over the rear of M^1; and the glenoid cavity is situated high on the side of the skull. Whitworth shows a slight notch between nasal and premaxilla; I was unable to detect this in the specimen. The palate is unfortunately not visible. The myohyracine mandible, if allowance be made for the increased depth beneath the hypsodont cheek teeth, is decidedly macroscelidid in appearance. The symphysis is short and shallow; the ascending ramus high and steeply rising, and the coronoid process small; the condyle is high and not expanded transversely; and the angle is hook-like and extended posterodorsally.

$P^2 - M^2$ of *Macroscelides* and *Nasilio* resemble the corresponding teeth of *Myohyrax* in a number of respects. The posterior cheek teeth of myohyracines are somewhat bowed outwardly (Whitworth, 1954, pl. 6, fig. 2), $P^2 - M^1$ are inclined backward and $P_3 - M_2$ are inclined forward; the bowing is incipient and the pitching definitely present in *Macroscelides*. M^2 of myohyracines is unreduced, in correlation with the retention of M^3_3; in *Nasilio*, in which M_3 is retained, the posterior portion of M^2 is less reduced than in the other living forms. The great reduction of M^3_3 is, of course, a decided resemblance to the macroscelidids and a striking contrast to the hyracoids. The crown pattern of the upper molars of the myohyracines (Fig. 5) is basically macroscelidid and not hyracoid in such characters as the large, external paracone and metacone, the absence of a mesostyle (in this I agree with Andrews and with Hopwood, believing Whitworth's mesostyle to be the paracone), and the position and relations of the lophs. In macroscelidines, especially *Macroscelides* and *Nasilio*, the lophs are relatively high, the protoloph going to the parastyle, the robust metaloph primarily to the paracone; the protocone is connected posteroexternally to the enlarged anteroexternal portion of the metaloph and the posteroloph is transverse, connecting metastyle and hypocone, all very much as in myohyracines. Between paracone, protoloph, metaloph and protocone anteriorly, and between metacone, metaloph and posteroloph posteriorly, two fossettes are isolated. These are aligned anteroexternally to posterointernally, and are the homologues of the anterior and posterior pairs of fossettes in the upper molars of myohyracines. In unerupted or little worn molars of *Macroscelides* tendencies toward division of each of these fossettes into two may be seen.

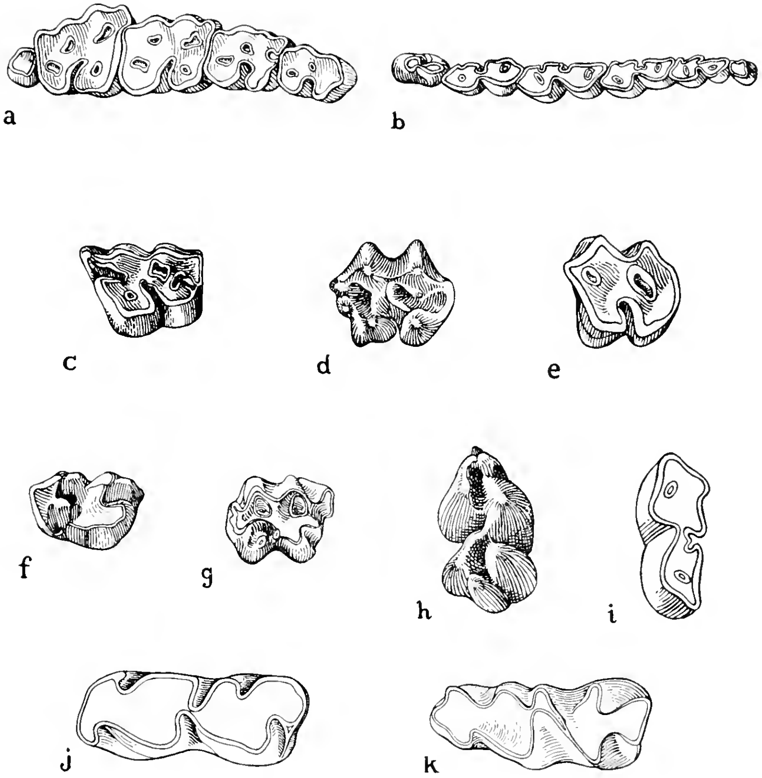

Figure 5. A comparison of myohyracine and macroscelidine cheek teeth. *Myohyrax oswaldi*: *a*, $P^3 - M^3$; *c*, M^2; *f*, dm^4; *j*, dm_4. *Protypotheroides beetzi*: *b*, $P_2 - M_3$; *i*, M_1. *Macroscelides proboscideus*: *d*, M^1 (unworn); *e*, M^1; *g*, dm^4; *h*, M_1 (unworn); *k*, dm_4. *a*, *b*, *c*, *f*, *i* redrawn from Stromer, *j* from Whitworth; *d*, *g*, *h*, *k* MCZ 37022, *e* MCZ 37023. *b* ×2; *a*, *c*, *f*, *i* ×4; *j* ×6.6; the rest not to scale.

The crown structure of P_4 and of the lower molars is close to that of *Palaeothentoides* and *Macroscelides* (Fig. 5). The lingual reëntrant between trigonid and talonid is less open than in these forms, and this narrowing was probably brought about by a swelling on the entoconid crest similar to but larger than that present in *Palaeothentoides*. *Macroscelides* has fossettids in the trigonids and talonids of unworn molars and these are closely comparable, although much shallower than those occurring in *Protypotheroides*.

The fourth upper milk molar of *Myohyrax* (Fig. 5f), like the permanent molars, is very similar to the corresponding tooth in macroscelidines. The differences that exist between it and that of, e.g., *Macroscelides* — parastyle less set off by grooves, more prominent posteroloph, nearly straight lingual wall, protocone not set off by an anterior groove — do not disguise the basic resemblance. Dm_4 of *Myohyrax* (Fig. 5j), although considerably worn, is again unmistakably macroscelidid in structure and quite unlike that of hyracoids. As in all members of the family, it is very long and low-crowned, with trigonid and talonid approximately equal in length. The paraconid area is set off by external and internal grooves from the large protoconid and the even larger metaconid, which was almost certainly twinned as it is in *Macroscelides.* The paraconid was clearly anterocentral in position with a short labial crest and a longer lingual one terminating in a parastylid. Lingual and labial reëntrants between trigonid and talonid are essentially as in *Macroscelides.* The hypoconid is very large; the entoconid and hypoconulid have become united by wear, while the groove between hypoconid and hypoconulid still persists. With wear this would occur in *Macroscelides.* An entostylid is present anterior to the entoconid, set off by grooves from it and from the metaconid; a precisely similar structure occurs in dm_4 of *Petrodromus.* I differ from Whitworth as regards cusp homologies in this tooth. My parastylid is his paraconid, my entoconid and hypoconulid are regarded by him as a stylar development and my entostylid is his entoconid. In hyracoids, dm^4 is somewhat narrower relative to length than is M^1, which it otherwise resembles very closely, and dm_4 and M_1 are nearly identical.

Stromer (1926) described and figured various postcranial fragments, which he referred to *Myohyrax.* Except for an atlas, which may not be correctly identified, all of these are decidedly macroscelidid in appearance. Figure 6 shows a selection of these fragments, redrawn from Stromer, compared with corresponding parts of a living member of the family. The resemblances are obvious and do not need to be elaborated. One point may be stressed. The astragalus is about as different as possible from that of hyracoids. This element in the latter is as distinctive in its way as are the corresponding bones of artiodactyls and perissodactyls. In the hyracoid astragalus the articular area of the trochlea continues distally over the medial side of the short neck into a curious, step-like surface for the reception of the long, stout internal malleolus of the tibia. This specialization had already been attained by early Oligocene, Fayum forms, the earliest known

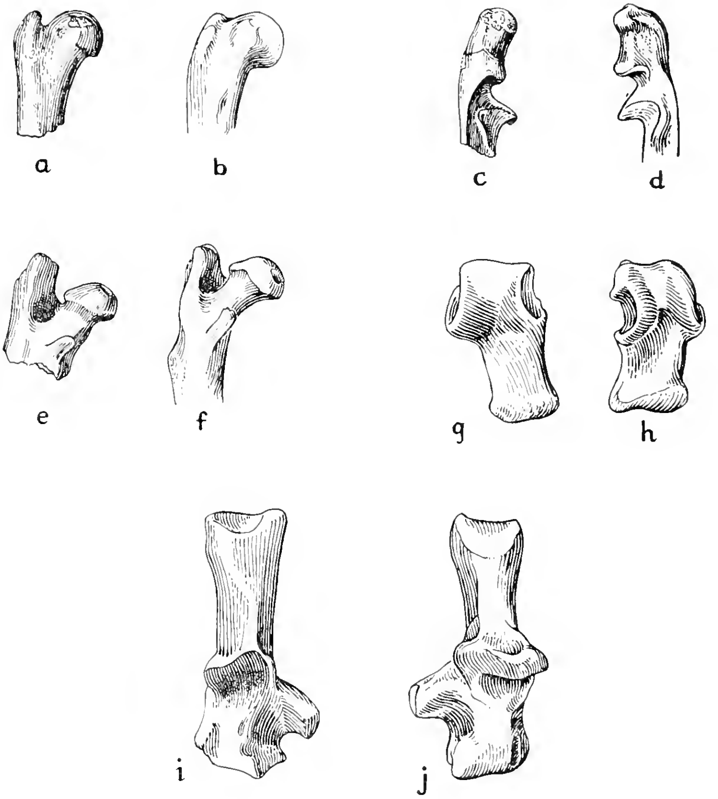

Figure 6. A comparison of myohyracine and rhynchocyonine postcranial elements. *Myohyrax oswaldi: a, c, e, g, i*; *Rhynchocyon cirnei*: *b, d, f, h, j*. *a, b*, proximal ends of humeri; *c, d*, proximal ends of ulnae; *e, f*, proximal ends of femora; *g, h*, astragali; *i, j*, calcanea. *a, c, e* ×2; *g, i*, ×4; *R. cirnei* not to scale. *M. oswaldi* redrawn from Stromer, *R. cirnei* MCZ 43735.

members of the order (Schlosser, 1911, p. 126, pl. 13, fig. 2). The comparatively long-necked myohyracine astragalus shows no trace of such a structure, and agrees in all essentials with those of other macroscelidids (Fig. 6 g, h). It is regrettable that none of these pieces is complete enough to give any idea of the degree of fusion of the lower leg bones, not to mention the relative lengths of the limb segments or of the fore and hind limbs. Whether or not the myohyracines were saltatorial, as are living forms[1], remains unknown.

Four species of early Miocene myohyracines have been described: *Myohyrax oswaldi* Andrews 1914, *Protypotheroides beetzi* Stromer 1922, *Myohyrax doederleini* Stromer 1926, and *Myohyrax osborni* Hopwood 1929. Of these, *M. oswaldi* and *M. doederleini* are small and very similar, *P. beetzi* and *M. osborni* are much larger and very similar. Whitworth recognizes but two species, *oswaldi* and *beetzi*, and in this he is undoubtedly correct. He goes on to synonymize *Protypotheroides* with *Myohyrax*, but here I am unable to follow him. It appears to me that the differences between the two valid species, summarized in the diagnoses below, are of generic significance, as genera are defined in this family.

MYOHYRAX Andrews

Myohyrax Andrews, 1914, p. 171.

Type species: M. oswaldi Andrews, 1914.

Distribution: Early Miocene, east and southwest Africa.

Emended diagnosis: Myohyracines with cement in fossettes of cheek teeth; M^3 single rooted; fossettids on $P_3 - M_2$ ephemeral.

MYOHYRAX OSWALDI Andrews

Myohyrax oswaldi Andrews, 1914, pp. 169–171, pl. 28, figs. 4–6; Stromer, 1926, pp. 123–124, pl. 41, figs. 26–28; Whitworth, 1954, pp. 26–40, text-figs. 9–15, pl. 5, figs. 3–4, pl. 6.

Myohyrax doederleini Stromer, 1926, pp. 120–123, text-fig. 19, pl. 41, figs. 1–23; Hopwood, 1929, p. 6, text-fig. 4.

Horizon: Early Miocene.

Localities: Kenya: Koru (type locality), Karungu, and Rusinga Island (definitely recorded from the lower Hiwegi beds); South-West Africa: Elisabethfelder, a borehole some 37 km SSE of Lüderitzbucht (Stromer), and "south of Lüderitz Bay" (Hopwood).

Diagnosis: As for the genus. Intermediate in size between the species of *Petrodromus* and those of the smaller macroscelidine genera.

The combination of relatively persistent fossettes in the upper molars and ephemeral fossettids in the lower molars is almost precisely matched in *Macroscelides*. The species is common at

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[1] It is sometimes stated (e.g. Evans, 1942, p. 85) on the basis of observations by field workers that, despite their evident saltatorial adaptations, macroscelidids do not hop but run on all four feet. Run they obviously do but hopping has also been observed.

certain localities. In South-West Africa, Stromer records over 100 from Elisabethfelder, and Whitworth (1958, p. 47) lists 120 from Karungu in Kenya.

PROTYPOTHEROIDES Stromer

Protypotheroides Stromer 1922, p. 333.

Type species: P. beetzi Stromer, 1922.

Distribution: Early Miocene, southwest Africa.

Emended diagnosis: Myohyracines without cement in fossettes of cheek teeth; M^3 two rooted; fossettids on $P_3 - M_2$ deep.

PROTYPOTHEROIDES BEETZI Stromer

Protypotheroides beetzi Stromer, 1922, p. 333; 1926, pp. 124–125, pl. 41, figs. 29–31.
Myohyrax osborni Hopwood, 1929, pp. 6–8, text-figs. 5–6.
Myohyrax beetzi Whitworth, 1954, p. 26.

Horizon: Early Miocene.

Localities: Langental, some 10 km NNE of Bogenfels (Stromer), and "south of Lüderitz Bay" (Hopwood), South-West Africa.

Diagnosis: As for the genus. A large species, for this family; comparable in size to *Rhynchocyon petersi* the largest living form.

Neither Stromer nor Hopwood mention cement in *P. beetzi*, and I was unable to detect any. The anterior wall of the alveolus of M^3 is preserved in the type of "*M. osborni*" and shows the presence of two roots. The fossettids extend nearly to the bases of the posterior cheek teeth. *P. beetzi* is rare in comparison with *M. oswaldi*, only eight specimens having been recorded.

DISCUSSION

INTRAFAMILIAL RELATIONSHIPS

Among the living forms, *Rhynchocyon* stands apart in a number of characters — e.g., largely or wholly edentulous premaxillae, upper canines large and P_1 caniniform, long and broad facial region, large cranial table, no palatal fenestrae, backwardly sloping ascending ramus, presence of chevron bones, radius and ulna not fused, digit I lacking and digit V reduced in the manus. The majority of authors agree in placing *Rhynchocyon* in a distinct subfamily and this seems justifiable. The extinct *R. clarki* shows that the subfamily was in existence by Miocene time, and in so doing provides us with the nearest approach to a phyletic lineage that we have. This species, as is not surprising, possesses some macroscelidine characters; divergence of the two subfamilies may date from earlier Oligocene time.

The Macroscelidinae, with four living and two extinct genera, form the core of the family, so far as present knowledge goes. The various forms differ unevenly within rather narrow limits. The heights of the cheek teeth range from brachyodont in *Metoldobotes* and *Petrodromus* to subhypsodont in *Palaeothentoides, Nasilio* and *Macroscelides,* yet two of the higher crowned forms, *Palaeothentoides* and *Nasilio,* are primitive in their retention of a vestigial M_3 (*Metoldobotes,* the earliest known macroscelidid, had already lost this tooth). *Macroscelides* stands alone in its possession of highly inflated bullae and epitympanic sinuses. *Nasilio,* advanced as regards molar height, has the tibia shorter relative to the femur than in either *Elephantulus* or *Macroscelides* and resembles in this respect the rather generalized *Petrodromus.* The latter, in turn, is specialized as regards the loss of the hallux, and so on. *Palaeothentoides* and the living macroscelidines give the impression of being terminal twigs of a once more numerous and varied group. It is unsafe at present to assert that two or more members of the subfamily are closer to each other than to the rest phylogenetically, since characters in common could well have been achieved independently.

The two extinct groups, Myohyracinae and Mylomygalinae, best regarded for the present as subfamilies, are highly specialized as regards their cheek teeth, the former in an ungulate-like, the latter in a rodent-like direction. Unfortunately, we know them only at moments in time — the two myohyracines in the earlier Miocene, *Mylomygale* in the Pleistocene — and hence have no direct evidence bearing on their phylogenies. The myohyracines, which alone in the family retain M^3 as well as M_3, may have branched off at an early date, possibly Eocene, the mylomygalines perhaps somewhat later. The ancestry of both groups may have lain in the Macroscelidinae, but this is uncertain.

The only extra-African form that has been referred to the family is *Pseudorhynchocyon cayluxi* Filhol (1892) from the Quercy Phosphorites. This very unsatisfactorily known animal was based on the posterior part of a left mandible, in which the alveoli of the last molar provide the only trace of the dentition. The ascending ramus is much inclined posteriorly, and Filhol saw in this a resemblance to *Rhynchocyon*. In fact, however, *Pseudorhynchocyon* in this respect goes far beyond conditions in the living form (Fig. 7). As Butler and Hopwood have pointed out, the ascending ramus of the Miocene *R. clarki* is considerably less inclined than in the

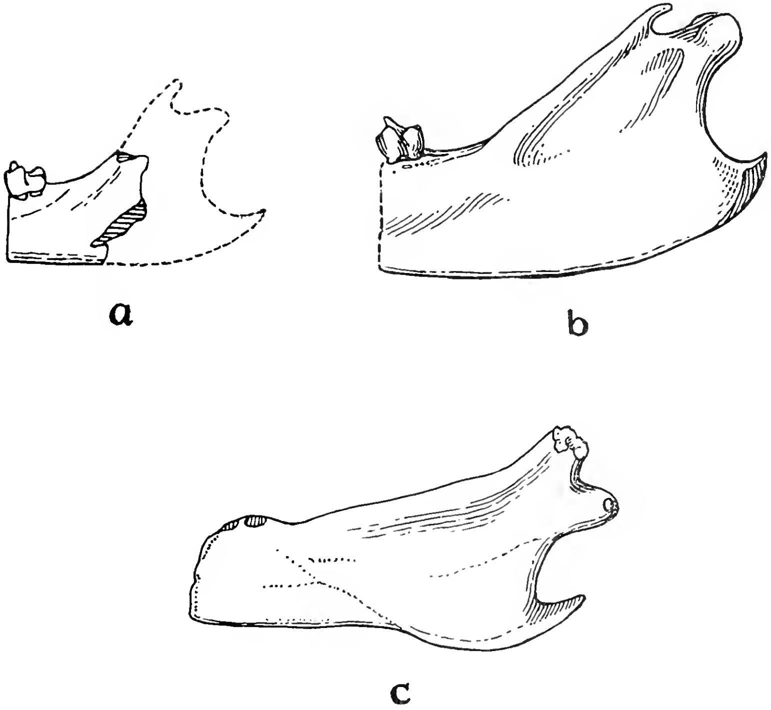

Figure 7. Posterior portions of mandibles of, *a*, *Rhynchocyon clarki*, *b*, *Rhynchocyon petersi*, *c*, *Pseudorhynchocyon cayluxi*. ×2. *a* modified from Butler and Hopwood, *b* MCZ 22573, *c* redrawn from Filhol.

living species, which suggests that such inclination is of relatively recent acquisition within the subfamily. Besides this, there is nothing at all macroscelidid-like about the structure of the ascending ramus of *Pseudorhynchocyon*. The coronoid process is much stouter than in any member of the family and extends well above the condyle. The latter faces posteriorly and is level with the cheek teeth, not far above them. The angle is low, and a prominent masseteric crest leads downward and then upward from it, projecting down below the level of the ventral border of the horizontal ramus. Butler and Hopwood conclude that ". . . the reference of *Pseudorhynchocyon* to the Macroscelididae is most improbable." They are quite right. Whatever the creature may be — and I can offer no constructive suggestion on this score — it is not a member of this wholly African family.

The Food of Macroscelidids

The posterior cheek teeth of myohyracines are comparable as regards degree of hypsodonty and crown complexity to those of certain hypsodont notoungulates, or, in miniature, to those of late Miocene or early Pliocene Equinae. As both Hopwood and Whitworth emphasize, such specialization can only be regarded as an adaptation to a diet consisting in large part of harsh vegetation. *Mylomygale* has posterior cheek teeth that are similar in height and complexity to those of various hypsodont rodents. Within the Macroscelididae there have arisen two groups primarily adapted to an abrasive vegetable diet. It thus becomes important to ascertain if living members of the family are to some extent herbivorous.

Structurally, as has long been recognized, the macroscelidid jaw is basically that of a herbivore. The jaw muscles, especially M. temporalis, show resemblances to those of artiodactyls, although, as Fiedler (1953, p. 161) has pointed out, the disposition of the tendons (Sehnenskelet) is "insectivoran." The structure of the cheek teeth, particularly of the higher-crowned living forms, is consistent with a diet at least partially herbivorous. Is there evidence that these animals do in fact eat plants? Regrettably, no thorough study of the diet of any macroscelidid is available, and the anecdotal literature is unsatisfactory. Unsubstantiated assertions to the effect that macroscelidids are exclusively insectivorous are common. Reports by collectors that insects were found in stomachs are sometimes quoted, but insect remains are relatively easy to detect and would likely be looked for (macroscelidids being "insectivores"), whereas vegetable remains, if scanty, are more difficult to recognize and might even be passed over without comment on the supposition that they had been accidentally ingested together with the prey. Nevertheless, a few statements do suggest that these animals are omnivorous. Thus, Sclater (1901, p. 155) states, on the authority of Francis, a collector, that *Petrodromus sultan* is ". . . very partial to the droppings of the Livingstone buck (*Nesotragus livingstonianus*)." Shortridge writes, of *Elephantulus* (1934, p. 21), ". . . although mainly insectivorous [they] are to some degree omnivorous, and may be caught in traps baited with mealies, quaker oats, etc."; and, of *E. intufi*, "examined stomach contents: insects and a small amount of vegetable matter" (p. 23). "The smaller species . . . feed mainly on ants . . . supplemented by tender shoots, roots and berries" (Walker *et al.* 1964, p. 134). The most convincing statement is by Broom (1898, p. 68): "*Macroscelides*[1], the Elephant-shrew, has a jaw which judging by analogy would certainly be related to a herbivorous form and the molar teeth would seem to be quite in harmony with this determination, and yet though *Macroscelides* is *largely a vegetable feeder* [italics mine] I have found in the stomach abundant remains of ants and even of fairly large beetles." Although quite inadequate to reveal how large a role vegetable food may play in the macroscelidid diet, this small budget of information does reveal that plants in one form or another are eaten. If early members of the family were similarly omnivorous, the evolution of predominantly herbivorous phyla is readily understandable.

The Systematic Position of the Macroscelididae

Real knowledge of the macroscelidids dates from 1829[2], when *Macroscelides* was described by Smith, and of the tupaiids from 1821[2], when Raffles proposed *Tupaia*. Neither group formed part of Bowdich's Insectivora of 1821, based on Cuvier's "les insectivores" of 1817, which included representatives of a majority of the living families. Given the knowledge available in the earlier part of the 19th century, however, it was inevitable that both families would be placed in this order. As knowledge improved it was equally inevitable that differences between them and the rest of the Insectivora would become increasingly apparent. Peters (1864), recognizing this, divided the order Insectivora into two major, unnamed groups, one with, one without a caecum, and included the colugos with the tupaiids and macroscelidids in the first. Haeckel (1866, p. cix), excluding the colugos, gave to these groups the formal names Menotyphla and Lipotyphla, the former based equally on the Cladobatida (= Tupaiidae) and the Macroscelidea (= Macroscelididae)[3], the latter including the original Insectivora.[4] With this, a stage was set. Elephant shrews and tree shrews became firmly associated in the minds of many investigators, and discussions of affinities, particularly of the former group, fell into a

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[1] The old inclusive genus *Macroscelides* had not been subdivided at this date, and the question therefore arises as to whether Broom was dealing with the genus as now restricted. It is known, however, that in 1897–98 he resided in Little Namaqualand and hence was within the range of *M. proboscideus*.

[2] *Macroscelides* had been known since 1800, but disguised as *Sorex proboscideus*, *Tupaia* since 1820, but disguised as *Sorex glis*.

[3] Simpson (1931, p. 16n; 1945, pp. 176, 183) has stated that Menotyphla was based on the macroscelidids; this does not appear to be the case.

[4] There is some tendency nowadays to employ Lipotyphla as an ordinal name for the Insectivora minus the "Menotyphla." It needs to be emphasized, as McKenna (1963b, p. 4n) has done, that "Lipotyphla" is to all intents and purposes strictly synonymous with Bowdich's Insectivora.

rut. The characters the two families had in common were hailed as proof of close relationship, almost as though the possession of such things as caeca and normal mammalian zygomatic arches and pubic symphyses were peculiar to them. Even after attention had become focused on the evident resemblances to primates shown by the tree shrews and strong doubts had been cast on the reality of Haeckel's Menotyphla, some students continued to associate the two families closely, and even to waft the macroscelidids to the primate heights as a kind of ill-fitting tail to the tupaiid kite.

Inclusion of the Tupaiidae in the Primates is a view becoming more and more widely accepted. There is no occasion here to trace the development of this concept (Carlsson, 1909, 1922; Gregory, 1910; Le Gros Clark, 1934; Simpson, 1935, 1945; and others) or to review the imposing body of data that favors it. Some items of evidence that have not yet passed into the general literature may be mentioned, however. Henckel (1928) and Roux (1947) concluded that the chondrocranium of *Tupaia* excluded the family from the order Primates. This opinion was largely based on the absence of a septum interorbitale, a supposed hall mark of primates. Grassé (1955, p. 1649), who recognized Menotyphla in the Haeckelian sense, utilized this to offset Saban's (1956–7) conclusion, based on a thoroughgoing study of the adult skull, that tupaiids were members of the order. Recently, Starck (1960, 1962), working on a wide variety of primates, has found the septum interorbitale to be a highly plastic structure without taxonomic significance, its presence or absence largely depending on the developmental stage under investigation. As he puts it, "Damit verlieren die Hypothesen (Henckel), die *Tupaia* aus der Primatenreihe ausschliessen wollen, ihre Hauptstütze."[1] The placentation of tupaiids was very poorly known until quite recently. Meister and Davis (1956) have helped to fill this gap with their description of three stages in *Tupaia minor*. They conclude that "morphologically the placenta and other fetal membranes of *Tupaia* are almost an ideal starting point from which to derive the corresponding structures of the primates." Of particular interest for the present study is their further conclusion, based on comparison with Van der Horst's drawings (1950) of *Elephantulus*, that ". . . the placenta and fetal membranes in these two forms differ in almost every respect except placental type"; the data ". . . support the view that the tree-shrews and elephant shrews are not

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[1] Since this was sent to press, W. Spatz' study of the ontogeny of the cranium of *Tupaia glis* (Morphol. Jahrb., 106: 321–416, 1964) has come to hand. He concludes that on this evidence tupaiids are primates.

closely related." The little evidence available on ectoparasites supports primate affinities for the former but not for the latter (Patterson, 1957, pp. 23, 26). A few uncertainties remain concerning the propriety of including tupaiids in the Primates. Some see the structure of the hand as a bar to inclusion while others do not. Buettner-Janusch and Buettner-Janusch (1964, p. 87) find that the electrophoretic behavior of the hemoglobin differs from that of other prosimians.[1] Jane, Campbell and Yashon (1965) have shown that in *Tupaia* the pyramidal tract occurs in the dorsal funiculus of the spinal cord, whereas in insectivores it occurs in the ventral funiculus and in primates in the lateral.[2] However, only one other prosimian, *Nycticebus,* has thus far been studied in this connection. A wider investigation may reveal that the distinction is not a clear cut one. It should be recalled, to introduce a note of caution, that until 1952 *Tupaia* could be said to differ from all primates in its possession of an outer bar of Jacobson's cartilage. In that year Eloff demonstrated the presence of the bar in *Galago senegalensis.* Certain facts do, of course, await further assessment, but the weight of the evidence now decidedly favors the ordinal reference; the burden of proof has shifted.

The Macroscelididae, to anticipate a little, are without much doubt a very ancient family that probably arose early in the Cenozoic, possibly even toward the end of the Mesozoic. In some respects specialized, they are nevertheless basically rather primitive. It is not surprising therefore that they should to varying degrees resemble other groups of mammals of more or less comparable antiquity. These resemblances, particularly those to the Insectivora and to the tupaiid primates, have been interpreted as indicative of close affinity to one or the other of these groups, wrongly interpreted I now believe.

As regards the soft anatomy, Le Gros Clark (1933, p. 1004) has stated of the brain that ". . . it would be difficult to conceive two small mammalian brains which are more fundamentally different and divergent in their structure than those of *Macroscelides* and *Tupaia.*" Stephan and Spatz (1962) and Stephan and Andy (1964) also emphasize that the macroscelidid brain differs from those of Insectivora in various ways, notably in the much larger mesencephalon and hippocampus. The organ of Jacobson (Broom, 1902,

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[1] On the basis of serum protein comparisons Goodman (1963, p. 137) concludes: "Although evidence for a definitive taxonomic assignment of the tree shrews has not been gathered, the serological data demonstrate that the tree shrews have affinities with the Primates. (Elephant shrews, placed by some taxonomists with tree shrews, do not show any primate or tupaiid affinities.)"

[2] In this, as in certain other respects, *Tupaia* may be simply primitive. The tract is dorsal in monotremes, marsupials, edentates and rodents.

1915) is of marsupial type, resembling that of *Tupaia* (presumably primitive in both groups) and very different from that of insectivores. Carlsson, although concluding that macroscelidids were close to erinaceids, did record certain characters in the musculature in which they resembled the tupaiids (1909, p. 396). The testes remain abdominal in elephant shrews, whereas the tree shrews have a well developed scrotum. Both, of course, have a caecum, but this is much larger in the elephant shrews. In sum, the evidence of the soft parts would appear to oppose close relationship to either the Tupaiidae or to the Insectivora.

The distinction between macroscelidids and tupaiids in placentation has been mentioned above (p. 324), as has the remarkable number of eggs liberated from the ovaries of certain of the Macroscelidinae (p. 307). The two families also differ as regards the young. In the elephant shrews these are decidedly precocial, being born fully haired, with the eyes open, and capable of active locomotion within a very short time (Hoesch and von Lehmann, 1956, p. 17; Walker *et al.* 1964, p. 135)[1]. In tree shrews — and also in the Insectivora generally (Herter, 1957, p. 31) — this is not the case. Uterine bleeding has been described by Van der Horst (1954, and references there cited) in *Elephantulus "myurus,"* with the suggestion that this foreshadows the menstrual cycle of the higher primates. The bleeding is of an unusual type, however. During diestrum a polyp-like growth forms in one part of the uterus and disintegrates at the end of the stage; coiled arteries, which are "enormously developed," are confined to this part. In all likelihood this is simply another macroscelidid peculiarity.

The dentition of macroscelidids, particularly the posterior cheek teeth, is unlike that of any other group of mammals. Carlsson saw resemblances to the teeth of Erinaceidae, but these are not close. The Macroscelididae have at times been placed in the Insectivora "Dilambdodonta" although there is nothing whatsoever dilambdodont about their molars. Frechkop (1931) has stated that the cheek teeth resemble those of ungulates more than those of any other major group. This is correct — the myohyracines evolved molars so ungulate-like as to mislead some very competent students — but there is no detailed similarity to any particular group of

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[1] A very curious observation concerning the young of *Elephantulus rupestris* has been reported. Fitzsimons (1920, pp. 12–13) quotes an observer, van Musschenbroek, who noticed that the two young ". . . were hanging on to something on top of the shoulder blades. On examination I found they were two teats, one on either side. [The mother] carried them by these teats [and] took good care to see that they were hanging on before she hopped away like a miniature kangaroo." As regards the position of the teats confirmation is supplied by Burton (1955), who states that Hayman found them to be situated high on the flanks just behind and above the scapulae.

hoofed mammals. The resemblance is an interesting example of convergence, as Friant (1935) concluded. On the basis of his observations, Frechkop asserted that the macroscelidids were on the ungulate road, just as the tupaiids were on the primate one. In this, of course, he went too far. All, or practically all, ungulate orders have surely emerged from the Condylarthra (to which the Arctocyonidae properly belong), and there is nothing suggestively condylarthran in the elephant shrews. Nevertheless, the myohyracines do raise the possibility that placental mammals could achieve "ungulate" grade independently of that order.[1] The dentition of the extinct macroscelidids gives no hint as to relations with any other group. The earliest known form, *Metoldobotes*, had the typical pattern and had lost the last molar.

The most recent study of the skeleton of the Macroscelididae is that of Evans (1942), who compared representatives of all genera except *Macroscelides* (see p. 309) with those of *Tupaia* and *Echinosorex*. He concluded that the macroscelidids resembled *Tupaia* in 30 osteological features and *Echinosorex* in 13. Further, he claimed that out of 40 lemuroid features mentioned by Gregory and by Carlsson as occurring in *Tupaia*, the macroscelidids shared in 32. This "simple morphological balance," as Simpson (1945, p. 176) called it, has been seized on as evidence for the reality of Menotyphla *sensu* Haeckel (e.g. Grassé, 1955, p. 1649; Heim de Balzac and Bourlière, 1955, p. 1691). It does not provide such evidence. Evans' study is in fact a classic example of the "rut discussions" mentioned above. He has shown beyond question that tupaiids and macroscelidids differ in a number of features, some of them more or less similar, from *Echinosorex*, which, as a true insectivore, has various characters not found in other major groups of mammals. This is a far cry from proving a close relationship between elephant shrews and tree shrews, however. Looking beyond the restricted prosimian-tupaiid-macroscelidid-insectivore circle, it becomes apparent at once that few of Evans' characters in common between tupaiids and macroscelidids are confined to these families. Furthermore, the resemblance between the two in many of the features cited is far from close. Some of the common features, e.g. the relatively large braincase, were in all probability independently acquired (the braincases at least house very dissimilar brains); others, e.g. the structure of the orbitotemporal region and of the zygomatic arch, are simply primitive eutherian, or therian, characters inherited by both; others again,

[1] The only other possible candidates for such a distinction that I can think of are the notoungulates. I am not suggesting a macroscelidid-notoungulate relationship!

e.g. the presence of a free centrale and of a third trochanter on the femur, are characters so widely possessed as to be meaningless in this context; yet others, e.g. large auditory bullae and slender coronoid process of the mandible, are not sufficiently similar structurally to qualify as significant resemblances; and so on. The same applies to the features cited as occurring in common between macroscelidids and lemuroids. Butler (1956, p. 476) has listed certain cranial characters in which the Macroscelididae, Dermoptera, Tupaiidae and Lemuroidea resemble each other. Some of these features are of the same sort as those cited by Evans. As regards the Macroscelididae, at least, they are equally open to question, as Butler recognized. The evidence from the hard parts seems to me to point in the same direction as that from the soft: namely, that the macroscelidids are sharply distinct from both Tupaiidae and Insectivora. Resemblances to ungulates do exist — *Rhynchocyon* and *Orycteropus* are remarkably similar in the disposition of the bones in the orbitotemporal region (cf. figs. 124 and 177 in Gregory, 1920), the rostral and caudal entotympanics of elephant shrews compare rather closely with those of notoungulates, fusion of distal elements in the limbs occurs in macroscelidids and in hoofed mammals, the astragalus has a fairly long neck in some small and primitive ungulates, etc. — but these appear to be either convergent or simply primitive in both.

Evans concluded, on the basis of superficial resemblances, that *Anagale* from the early Oligocene of Mongolia ". . . is, in many osteological features, intermediate between the Macroscelidae and the Tupaiidae and is either the common ancestor of the two families or quite close to it." New evidence, derived from a hitherto undescribed specimen of *Anagale*, and from *Anagalopsis*, reveals that the cheek teeth are quite different from those of either family, and that the tympanic forms the lateral portion of the bulla instead of being a ring enclosed by the entotympanic, as Simpson (1931) had supposed. Basing his conclusion on this evidence and on the very peculiar structure of the unguals, McKenna (1963a) has removed the Anagalidae from the Tupaioidea, where Simpson had placed them, and listed them as Eutheria *incertae sedis*. Whatever the anagalids may prove to be, they are not related to the macroscelidids. *Metoldobotes*, it may be recalled, was contemporary with *Anagale*.

As will by now be evident, I believe the elephant shrews to be a group of mammals distinct from both the Insectivora and the tupaiid primates. Their known distribution is exclusively African, and they make their first appearance in the record in the earliest adequately known mammalian fauna of that continent. They are accompanied there by an array of mammalian groups unknown elsewhere in deposits of earlier or similar date — hyracoids, arsinoitheres, moeritheres, barytheres, proboscideans and catarrhine primates. So notable a degree of endemism argues a long isolation of Africa[1] (Darlington, 1957, pp. 365, 590; Patterson, 1957, p. 45), one lasting throughout much of the Eogene at least. Macroscelidids may well have been members of this "old African" fauna, survivors from the later Cretaceous beginnings of the Eutheria. As a group they are more diversified and contain more genera than almost one-third of the currently recognized orders of eutherian mammals. They are, I believe, worthy of ordinal rank.

Butler (1956) has proposed for them the ordinal name Macroscelidea[2] without definition. Such action seems preferable to restriction of Menotyphla to the elephant shrews. Menotyphla has long had a proto-primate flavor, and since the tupaiid half of the artificial assemblage almost surely is primate and the macroscelidid half assuredly is not, it hardly seems desirable to attempt perpetuation of so ambiguous a name for the latter alone.

The order may be definied as follows:

MACROSCELIDEA

Dentition I^{0-3}_{3}, C^{1}_{1}, P^{4}_{4}, M^{2-3}_{2-3}; P^{4}_{4} large, molariform; upper cheek teeth without mesostyles; M^{3}_{3}, when present, greatly reduced; posterior cheek teeth brachyodont to hypsodont. Skull with complete zygomatic arch; orbits large, open posteriorly; maxilla not extending into orbital wall, palatine with orbital wing; auditory bulla compound, ectotympanic, rostral and caudal entotympanics, alisphenoid, squamosal, periotic participating; mandible with high ascending ramus, condyle well above level of cheek teeth, coronoid process small. Pelvis with pubic symphysis; humerus with entepicondylar foramen; distal segments of legs longer than proximal; radius and ulna fused or closely appressed, tibia and

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[1] When this isolation began and ended is of course uncertain. Darlington, on the basis of the rather few northern forms that occur in the Fayum deposits, believes that a connection had by then become established. This does not seem certain; that only two or three of a great many northern groups would have made their way over a land bridge had this been fully in existence is rather unlikely. The Fayum rodents belong to a family not known in Eurasia; they may well have descended from waif ancestors transported during the period of isolation.

[2] Somewhat vaguely, however, since in the body of his paper (p. 479) he expressed doubt as to the propriety of including the elephant shrews in the Insectivora ("Lipotyphla" in his terminology), suggesting that they should either ". . . be included in the Primates as an outlying suborder, or a new order, Macroscelidea, should be created for them." In the summary (p. 480) he simply remarked that they are ". . . placed in a new order, Macroscelidea." Haeckel's prior — and invalid (by modern standards) — use of the same name for the family does not constitute preoccupation. I was previously dubious about recognition of the order (1957, p. 23), but with the increase in knowledge of the fossil record my doubts have disappeared.

fibula fused; pollex and hallux reduced or absent; astragalar neck moderately long. Proboscis long, flexible; organ of Jacobson of marsupial type; brain with relatively large mesencephalon and specialized hippocampus; caecum relatively large; testes abdominal.

One family, Macroscelididae, with four subfamilies: Macroscelidinae, Rhynchocyoninae, Mylomygalinae, Myohyracinae.

Known range: Early Oligocene to Recent, Africa.

SUMMARY

The Macroscelididae, a wholly African group so far as known, includes four subfamilies, two of which are extinct. The Macroscelidinae date from the early Oligocene of the Fayum, where they are represented by *Metoldobotes*, a form originally referred to the insectivore family Mixodectidae. *Palaeothentoides* of the early Pleistocene(?), first described as a marsupial, is a valid member of the subfamily. Extinct species of *Elephantulus* are known from the Pleistocene. The early Miocene *Rhynchocyon clarki* provides the only fossil record of the Rhynchocyoninae. The subfamily Mylomygalinae is proposed for the Pleistocene *Mylomygale*, a remarkable form with hypsodont posterior cheek teeth convergent toward those of various rodents. The Myohyracinae, hitherto placed in the Hyracoidea as Myohyracidae or Myohyracoidea, are represented by the early Miocene *Myohyrax* and *Protypotheroides*. Their posterior cheek teeth are decidedly ungulate-like and comparable in complexity and degree of hypsodonty to those of Equinae and hypsodont Notoungulata. *Pseudorhynchocyon cayluxi* from the Quercy Phosphorites is not a member of the family.

The extinct subfamilies were beyond doubt predominantly herbivorous. Some evidence indicates that the surviving forms are to a degree omnivorous.

The affinities of the family are reviewed and the conclusion reached that macroscelidids are not closely related either to the tupaiid primates or to the insectivores. Resemblances to ungulates are either convergent or primitive. Butler's order Macroscelidea is recognized for the reception of the group and a definition is offered.

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By Arthur M. Chickering

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No. 7.—*Panamanian Spiders of the Genus* TMARUS (*Araneae, Thomisidae*)

BY ARTHUR M. CHICKERING

The Pickard-Cambridges (1889–1905) recognized seven species of *Tmarus* from Panama. Petrunkevitch (1925) reported only a single immature specimen of the genus from Panama. Banks (1929) reported two species now regarded as *T. ineptus* O.P.-Cambridge and *T. studiosus* O.P.-Cambridge. As a result of my earlier study of the genus (1950) I was able to recognize eighteen species. Four of these were known only from females, seven known only from males, with the remaining seven probably known from both sexes. Roewer (1954) listed twenty species known from Panama. This list includes *T. separatus* Banks and *T. interritus* Keyserling, but this inclusion seems to have been an error. *T. separatus* Banks is apparently known only from Mexico and *T. interritus* Keyserling only from Brazil. Since the publication of my previous paper on this genus (1950), I have collected spiders in Panama during four additional periods as a result of which I have accumulated a considerable number of specimens in this generic group. These have been completely worked over with the result that I am now compelled to recognize twelve additional species, thus making a total of thirty species known from this small area. It continues to be very difficult to match up males and females correctly and I am obliged to state that I have some doubts concerning the accuracy with which this has been done in the past.

As I have frequently stated in my published papers, I am deeply grateful for the many privileges extended to me by the staff of the Museum of Comparative Zoology, Harvard University, over a period of many years. My studies could never have been continued without this aid and encouragement. Special acknowledgements should be extended to Dr. Ernst Mayr, Director; Dr. P. J. Darlington, Jr., Alexander Agassiz Professor of Zoology; and Dr. Herbert W. Levi, Associate Curator of Arachnology.

Grant No. GB-1801 from the National Science Foundation made it possible for me to spend seven months making collections of spiders in the West Indies and Panama during the latter part of 1963 and the first five months of 1964. This grant is also making it possible for me to continue my studies at the Museum of Comparative Zoology for a considerable period. A Guggenheim Fellowship made it possible for me to collect in Jamaica, W. I., and in Panama, in 1957 and 1958, and also to spend four months in the

British Museum (Natural History) studying important collections. Dr. G. Owen Evans and Mr. D. J. Clark, Department of Zoology (Arachnida), British Museum (Natural History), have recently loaned me important specimens of the genus *Tmarus* for study in the preparation of this paper.

All types named in this publication together with all other specimens of the genus *Tmarus* in my personal collection will be deposited in the Museum of Comparative Zoology, Harvard University.

Genus TMARUS Simon, 1875

The type species of the genus is *Tmarus piger* (Walckenaer), 1802; widely distributed in Europe and Asia. The genus is cosmopolitan in distribution and is most abundant in the neotropical region.

In addition to the general family characteristics, generic features common to the species from Panama may be stated as follows: Chelicerae without teeth; only slightly porrect; essentially parallel. Lip much longer than wide at base. Eyes: eight in two rows; viewed from above, posterior row definitely recurved, anterior row slightly so; lateral eyes larger than medians, on well defined tubercles; posterior tubercles the larger; central quadrangle usually wider behind than long and wider behind than in front. Clypeus porrect, often conspicuously so; height equal to several diameters of AME. Carapace usually abruptly declined to posterior border; without a median thoracic groove or fovea. Legs: spinose; usually 1243 in order of length but occasionally 2143 or other minor deviation; one and two nearly equal in length and longer than three and four which are also nearly equal in length. Tarsal claws toothed; palpal claw in females also toothed. Abdomen often with a posterior tubercle or other modification; with many short, stiff spines and spinules. Male palpi usually well supplied with apophyses, and female epigyna usually well defined and often complicated. To conserve space certain features possessed in common by all species under consideration will not be specifically mentioned in the technical descriptions of new species in this paper. For the same reason a more concentrated description than usual in my published papers will be adopted in this and succeeding publications. When eyes are referred to by the abbreviations AME, ALE, PME and PLE, the anterior medians, anterior laterals, posterior medians and posterior laterals are respectively designated.

A complete list of the species of the genus *Tmarus* from Panama as they are now recognized may be given as follows: *Tmarus aculeatus* Chickering; *T. bucculentus* Chickering; *T. cognatus* Chickering; *T. contortus* Chickering; *T. corruptus* O. P.-Cambridge; *T. cretatus* sp. nov.; *T. curvus* Chickering; *T. decens* O. P.-Cambridge; *T. decorus* sp. nov.; *T. humphreyi* sp. nov.; *T. impedus* sp. nov.; *T. ineptus* O. P.-Cambridge; *T. innotus* sp. nov.; *T. innumus* sp. nov.; *T. intentus* O. P.-Cambridge; *T. levii* sp. nov.; *T. longus* sp. nov.; *T. morosus* Chickering; *T. mundulus* O. P.-Cambridge; *T. obsecus* sp. nov.; *T. parki* Chickering; *T. pauper* O. P.-Cambridge; *T. peregrinus* Chickering; *T. probus* Chickering; *T. productus* Chickering; *T. protobius* sp. nov.; *T. rubinus* sp. nov.; *T. sigillatus* Chickering; *T. studiosus* O. P.-Cambridge; *T. vitusus* sp. nov. Ten of the species listed above are known only from males; ten species are known only from females; the remaining ten are probably known from both sexes.

Key to the males of known species of *Tmarus* from Panama

1. Species with embolus definitely and conspicuously curled either at anterior end of bulb on ventral side or on retrolateral side (*contortus, curvus, morosus, productus*) 2

1a. Species with embolus either extended more or less around the margin of bulb and not definitely curled or, apparently, restricted to anterior end of bulb (*aculeatus, cretatus, decorus, humphreyi, ineptus, innotus, intentus, mundulus, obsecus, parki, pauper, peregrinus, probus, sigillatus, studiosus, vitusus*) 5

2. Palpal tibial apophyses short, only ventral one strongly chitinized; cymbium deeply excavate at retrolateral basal corner; embolus deeply grooved, arises near middle of anterior border of bulb, makes a complete retrolateral circle and then loops across middle of bulb again (fig. 4, 1950) . . . . *T. contortus*

2a. Palpal features not as given above (*curvus, morosus, productus*) 3

3. Palp: tibia deeply excavate retrolaterally and distally; with a strongly chitinized apophysis of moderate length ventral to excavation; embolus makes a complete circle distal to anterior margin of bulb, then passes retrolaterally to terminate in a finely dentate tip (fig. 7, 1950) . . *T. curvus*

3a. Without palpal features as given above (*morosus, productus*) 4

4. Palp: ventral, retrolateral, tibial apophysis strongly chitinized and distally knobbed; dorsal apophysis a sharply pointed spine; near anterior margin of bulb the embolus turns toward base, then passes to retrolateral side and extends nearly to tip of cymbium as a long, slender filament (figs. 13–14, 1950) . . . . *T. morosus*

4a. Palp: with a pair of long, slender, retrolateral, tibial apophyses almost meeting distally, with a hook attached near base of the shorter apophysis; deeply grooved embolus makes a loop near distal margin of bulb, then a second loop near base of bulb, continues as a fine filament to distal end of cymbium (fig. 25, 1950) . . . . *T. productus*

5. Palp: species with at least the dorsal retrolateral, tibial apophysis elongated and well developed (*aculeatus, cretatus, decorus, humphreyi, parki, peregrinus, probus, studiosus, vitusus*) 6

5a. Palp: species with retrolateral tibial apophyses less well developed; either with but one apophysis or with two shorter and poorly developed apophyses (*ineptus, intentus, innotus, mundulus, obsecus, pauper, sigillatus*) 14

6. Palp: with a retrolateral, dorsal, tibial apophysis extending nearly to tip of bulb (*aculeatus, decorus*) 7

6a. Palp: with a retrolateral, dorsal, tibial apophysis extending at most little beyond middle of bulb (*cretatus, humphreyi, parki, peregrinus, probus, studiosus, vitusus*) 8

7. Palp: with the dorsal, retrolateral, tibial apophysis distally bifurcated (fig. 1, 1950) . . . . *T. aculeatus*

7a. Palp: with the dorsal, retrolateral, tibial apophysis simple at tip, not bifurcated (Figs. 7–8) . . . . *T. decorus*

8. Palp: with the dorsal, retrolateral, tibial apophysis subdivided near its base into a short, pointed process and a long, pointed extension (figs. 29–30, 1950) . . . . *T. studiosus*

8a. Palp: without any basal division of the dorsal, retrolateral, tibial apophysis (*cretatus, humphreyi, parki, peregrinus, probus, vitusus*) 9

9. Palp: with the dorsal, retrolateral, tibial apophysis definitely serrated along its external edge near middle (fig. 23, 1950) . . . . *T. probus*

9a. Palp: without any serration along external edge of dorsal, retrolateral, tibial apophysis (*cretatus, humphreyi, parki, peregrinus, vitusus*) 10

10. Palp: with the ventral, retrolateral, tibial apophysis a relatively massive structure, deeply notched at distal end (Fig. 10) . . . . *T. humphreyi*

10a. Palp: with the ventral, retrolateral, tibial apophysis relatively smaller and unnotched at its distal end (*cretatus, parki, peregrinus, vitusus*) . . 11

11. Palp: dorsal, retrolateral, tibial apophysis with two nearly right angles in its total length (fig. 20, 1950) . . . . *T. parki*

11a. Palp: with dorsal, retrolateral, tibial apophysis not provided with right-angled bends (*cretatus, peregrinus, vitusus*) 12

12. Palp: dorsal, retrolateral, tibial apophysis flask-like in shape (fig. 22, 1950) . . . . *T. peregrinus*

12a. Palp: dorsal, retrolateral, tibial apophysis not flask-like in shape (*cretatus, vitusus*) 13

13. Palp: dorsal, retrolateral, tibial apophysis elongated; ventral, tibial apophysis definitely hammer-headed (Figs. 1–2) . . . . *T. cretatus*

13a. Palp: dorsal, retrolateral, tibial apophysis robust, with a very slender terminal spine; ventral, retrolateral apophysis short, broad, slightly indented terminally . . . . *T. vitusus*

14. Palp: with a definitely recurved hook at base of tarsal bulb (fig. 28, 1950) . . . . *T. sigillatus*

14a. Palp: tarsal bulb without any definite recurved hook at its base (*ineptus, intentus, innotus, mundulus, obsecus, pauper*) 15

15. Palp: with a pair of short, pointed processes emerging from a rounded depression at anterior end of bulb (fig. 10, 1950) . . . . *T. ineptus*
15a. Palp: bulb without such structures as given above (*intentus*, *innotus*, *mundulus*, *obsecus*, *pauper*) 16
16. Palp: tarsal bulb with a single, bifurcated process emerging from a rounded depression at anterior end (F. P.-Cambridge's fig. 26, table 10) . . . . *T. intentus*
16a. Palp: tarsal bulb without such a structure as given above (*innotus*, *mundulus*, *obsecus*, *pauper*) 17
17. Palp: ventral, retrolateral, tibial apophysis a short, blunt process; considerably longer than very short, dorsal, retrolateral apophysis (figs. 16–17, 1950) . . . . *T. mundulus*
17a. Palp: tibial apophyses not as given above (*innotus*, *obsecus*, *pauper*) . . 18
18. Palp: both tibial apophyses short, bluntly pointed processes (O. P.-Cambridge's fig. 8, table 12) . . . . *T. pauper*
18a. Palp: retrolateral, tibial apophyses unlike those given above (*innotus*, *obsecus*) 19
19. Posterior fourth of abdomen sharply constricted but with no discernible tubercle (Fig. 27) . . . . *T. obsecus*
19a. Abdomen with no marked constriction; with a small but distinct dorsal tubercle in last quarter . . . . *T. innotus*

No satisfactory key has yet been devised to aid in the identification of females of known species from Panama.

TMARUS ACULEATUS Chickering

Tmarus aculeatus Chickering, 1950. Bull. Mus. Comp. Zool., 103(4): 217, fig. 1. The male holotype from Barro Colorado Island, C. Z., together with several male paratypes from localities in the Panama Canal Zone and nearby parts of Panama are all in the Museum of Comparative Zoology. Roewer, 1954; Bonnet, 1959.

Since 1950 the species has been taken only on Barro Colorado Island, C. Z., Summit, C. Z., and Arraijan, R. P. The female is still unknown.

TMARUS BUCCULENTUS Chickering

Tmarus bucculentus Chickering, 1950, Bull. Mus. Comp. Zool., 103(4): 220, fig. 2. The female holotype from Ft. Randolph, Panama Canal Zone, August, 1936, together with a female paratype, are in the Museum of Comparative Zoology. Roewer, 1954: Bonnet, 1959.

This species, known only from females, has been collected in three different localities in the Canal Zone since my publication in 1950.

TMARUS COGNATUS Chickering

Tmarus cognatus Chickering, 1950, Bull. Mus. Comp. Zool. 103(4): 222, fig. 3. The female holotype and two female paratypes from the Panama Canal Zone Forest Preserve, August, 1939, are in the Museum of Comparative Zoology. Roewer, 1954; Bonnet, 1959.

This species, also known only from females, has not been taken since the original specimens were collected.

TMARUS CONTORTUS Chickering

Tmarus contortus Chickering, 1950, Bull. Mus. Comp. Zool., 103(4): 224, figs. 4–5. The male holotype, female paratype, one male paratype and three immature specimens, all taken in the Madden Dam region, Panama Canal Zone, August, 1939, are in the Museum of Comparative Zoology. Roewer, 1954; Bonnet, 1959.

A very small number of both sexes have been taken since the establishment of the species and all have come from the Canal Zone Forest Preserve.

TMARUS CORRUPTUS O. P.-Cambridge

Tmarus corruptus O. P.-Cambridge, 1892, Arachnida-Araneida, 1: 95, pl. 12 fig. 10. The holotype female from Bugaba, Panama, is in the British Museum (Natural History). F. P.-Cambridge, 1900; Chickering, 1950; Roewer, 1954; Bonnet, 1959.

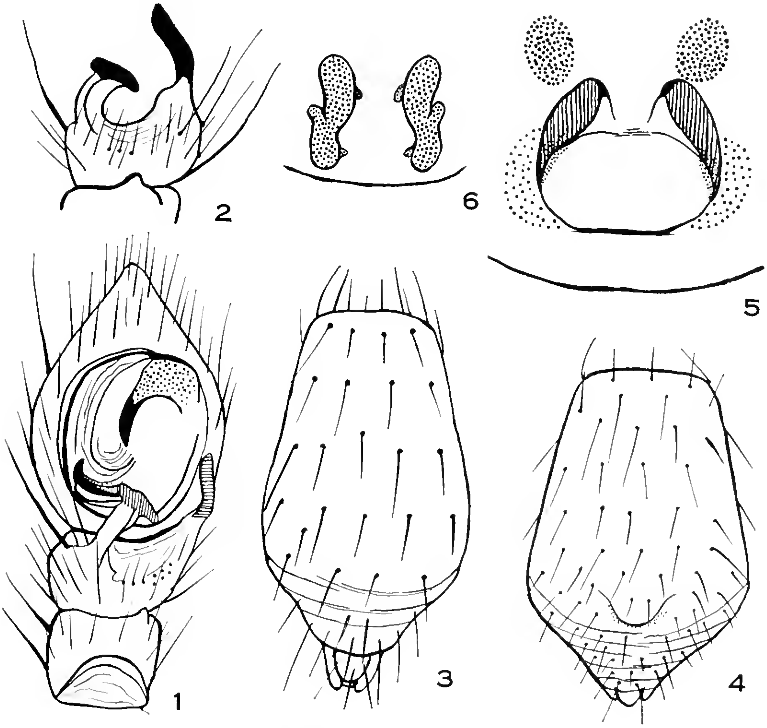
This species remains poorly known and only from females. The elder P.-Cambridge had the holotype from Bugaba, Panama; F. P.-Cambridge believed that he had the species from Mexico. It has not yet appeared in my collections. A female on loan from the British Museum (Natural History) does not show the two pairs of minute canals drawn so clearly by F. P.-Cambridge. O. P.-Cambridge's figure 10c, plate 12, is nearer to what I see in the epigynum than what is shown in F. P.-Cambridge's figure 32, plate 10. In view of the uncertainties here and the scarcity of material I am reserving further treatment of the species pending the acquisition of more specimens for a comparative study.

TMARUS CRETATUS sp. nov.

Figures 1–6

The specific name is a Latin adjective suggested by the chalky appearance of the body.

Male holotype. Total length, including slightly porrect chelicerae, 3.84 mm. Carapace 1.49 mm long, 1.56 mm wide opposite interval between second and third coxae where it is widest; 0.47 mm tall and, therefore, less than $\frac{1}{3}$ as tall as wide. Eyes: viewed from above, posterior row strongly recurved, anterior row gently so; central ocular quadrangle wider behind than in front in ratio of 13 : 10, longer than wide behind in ratio of 15 : 13; posterior row occupies about 9/13 of width of carapace at that level; ratio of eyes AME : ALE : PME : PLE = 5.5 : 12 : 4.5 : 13; AME separated from one another by nearly twice their diameter, from ALE by a little more than twice their diameter; PME separated from one another by a little less than four times their



Tmarus cretatus sp. nov.

Fig. 1. Left palp of male, ventral view.
Fig. 2. Left palpal tibia, retrolateral view.
Fig. 3. Dorsal view of abdomen of male.
Fig. 4. Dorsal view of abdomen of female.
Fig. 5. Epigynum, from below.
Fig. 6. Spermathecae of female paratype, cleared and turned outward to show internal arrangement.

diameter, from PLE by six times their diameter; laterals separated by 2¼ times the diameter of ALE. Height of clypeus equal to 4¼ times the diameter of AME. Legs 1234. Palp: essential features shown in Figures 1–2; tibial apophyses quite distinctive. Abdomen: posterodorsal tubercle, prominent in the female, appears here as only a slight rise. Color in alcohol: general chalky appearance important; first two pairs of femora with numerous white flecks on prolateral surfaces; venter of abdomen with a median, longitudinal, light brownish stripe and a narrow, white stripe on each side (in some paratypes the median stripe is nearly black).

Female paratype. Total length, including bases of chelicerae and slightly extended posterior spinnerets, 5.84 mm. Carapace 2.08 mm long, 2.21 mm wide opposite interval between second and third coxae where it is widest. Clypeus somewhat more porrect than in male; height equal to five times the diameter of AME. Legs 1243. Abdomen: with a prominent posterodorsal tubercle as indicated in Figure 4. Epigynum: essentially as shown in Figures 5–6. Color: essentially as in male; median, ventral, abdominal stripe is dark brown.

Type locality. The male holotype is from Summit, Panama Canal Zone, July, 1950; the female paratype was taken in the same locality in August, 1950. One male paratype was taken at Summit, C. Z., July, 1950; several female paratypes are in the collection from Summit, C. Z., July and August, 1950, and Summit Gardens, C. Z., August, 1954.

Tmarus curvus Chickering

Tmarus curvus Chickering, 1950, Bull. Mus. Comp. Zool., 103(4): 228, figs. 7–8. The male holotype and female paratype were taken on Barro Colorado Island, Panama Canal Zone, August, 1936. Paratypes of both sexes were reported from several localities in the Canal Zone and in Panama proper; all specimens are in the Museum of Comparative Zoology. Roewer, 1954; Bonnet, 1959.

The species has been collected during two recent collecting periods in the Canal Zone.

Tmarus decens O. P.-Cambridge

Tmarus decens O. P.-Cambridge, 1892, Arachnida-Araneida, 1: 98, pl. 12, fig. 9. The holotype female is in the British Museum (Natural History). F. P.-Cambridge, 1900; Chickering, 1950; Roewer, 1954; Bonnet, 1959.

This species, known only from the female, has not yet appeared in my collections and is known only from Bugaba, Panama.

TMARUS DECORUS sp. nov.

Figures 7–8

The specific name is a Latin adjective suggested by the decorative pattern on the cephalothorax and dorsal areas of the abdomen.

Male holotype. Total length, including somewhat porrect chelicerae, to tip of anal tubercle 4.39 mm. Carapace 1.69 mm long; 1.5 mm wide opposite second coxae where it is widest; about 0.68 mm tall and, therefore, less than half as tall as wide. Eyes: viewed from above, posterior row strongly recurved, anterior row slightly so; viewed from in front, anterior row almost straight, measured by centers; central ocular quadrangle wider behind than in front in ratio of about 16 : 11; about as wide behind as long. Ratio of eyes AME : ALE : PME : PLE = 5 : 11 : 6.5 : 10. AME separated from one another by nearly 2.5 times their diameter, from ALE by three times their diameter. PME separated from one another by slightly less than three times their diameter, from PLE by nearly 4.5 times their diameter. Laterals separated by nearly three times the diameter of PLE. Clypeus quite porrect; height equal to about seven times the diameter of AME (only chitinized area measured); apparently bearing only a single, slender spine at each ventrolateral angle. Sternum: sternal suture gently recurved; not extended between fourth coxae which are separated by about three-fourths of their width. Legs: 1243; with numerous long, slender spines. Palp: most essential features shown in Figures 7–8; patella and tibia short; the latter with two conspicuous apophyses. Abdomen: a slight swelling may indicate a more or less prominent posterodorsal tubercle in the female when the latter is known; with numerous long, slender spines; only a little more than twice as long as wide. Color in alcohol: carapace yellowish with red and pink decorations; a narrow red marginal band nearly encircles this part of the body from opposite the interval between LE to posterior border where there is a central gap in the colored margin; within the dorsal area there is an irregular, bright red figure consisting of a series of short radii surrounding a yellowish area; the clypeus bears a pair of relatively large, irregular, reddish spots; the chelicerae are yellowish with a central pink spot on each; legs basically yellowish but with many small red or pink dots and larger reddish blotches; fourth leg and, to a lesser extent, the third leg with the reddish dots united into narrow stripes especially on the patellae and tibiae; abdomen with a series of reddish and white transverse bands extending laterally and posteriorly; the venter is yellowish with a dusty brown center.

Type locality. The holotype male is from Barro Colorado Island, Panama Canal Zone, February, 1958. There are no paratypes and the female is unknown.

TMARUS HUMPHREYI sp. nov.
Figures 9–13

For some time the males and females here regarded as representing one species were considered as two. Recently, however, after studying the paratypes of both sexes it was decided that it would be safe to combine them. The species is named in honor of Richard L. Humphrey, M. D., a former student of mine and a delightful companion on an extended collecting trip in Panama.

Male holotype. Total length, including somewhat porrect chelicerae, 3.74 mm. Carapace 1.39 mm long, 1.19 mm wide opposite anterior border of first pair of legs; 0.55 mm tall and, therefore, a little less than half as tall as wide. Eyes: viewed from above, posterior row rather strongly recurved, anterior row gently so; viewed from in front, anterior row nearly straight, measured by centers; central ocular quadrangle wider behind than in front in ratio of 25 : 18, longer than wide behind in ratio of 27 : 25; posterior row occupies nearly four-fifths of width of carapace at that level. Ratio of eyes AME : ALE : PME : PLE = 5 : 10 : 6.5 : 9. AME separated from one another by twice their diameter, from ALE by a slightly greater distance. PME separated from one another by slightly more than twice their diameter, from PLE by about 3.5 times their diameter. Laterals separated by about twice the diameter of PLE. Clypeus: quite porrect; with seven long, slender spines along ventral border; height, including membranous border, equal to nearly six times the diameter of AME. Chelicerae and maxillae essentially typical of the genus. Sternum: bluntly terminated posteriorly and only slightly extended between fourth coxae which are separated by about two-thirds of their width; otherwise essentially typical of the genus. Legs: 1243. Palp: most essential features shown in Figures 9–11. Abdomen: almost squarely truncate at anterior dorsal border; a small posterodorsal tubercle is curved downward; dorsum with numerous slender spines each arising from a small, basal tubercle. Color in alcohol: carapace reddish brown with many irregular, dark, oblique stripes along lateral sides; legs yellowish with fine, black dotting; sternum brownish with darker spots extending from coxae toward the center; abdomen a dull black dorsally with a narrow, central, yellowish stripe extending through the anterior half; lateral sides of abdomen with alternating, irregularly narrow, dark and light stripes; venter with a broad, nearly black, central stripe and a narrow, irregular light stripe on each side.

Female paratype. Total length 5 mm, including bases of somewhat porrect chelicerae; carapace 1.76 mm long, 1.45 mm wide opposite second coxae, 0.84 mm tall and, therefore, a little more than half as tall as wide, with the usual supply of long, slender spines. Eyes: central ocular quadrangle wider behind than in front in ratio of 15 : 11; about as long as wide behind; ratio of eyes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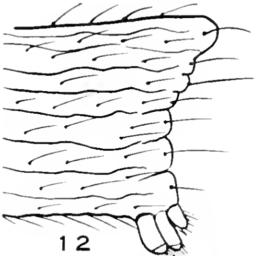
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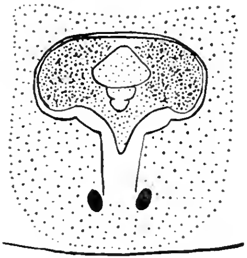
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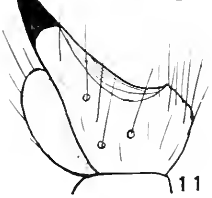
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Tmarus decorus sp. nov.

Fig. 7. Tibia and tarsus of left male palp, ventral view.
Fig. 8. Tibia and tarsus of left male palp, retrolateral view.

Tmarus humphreyi sp. nov.

Fig. 9. Tibia and tarsus of left male palp, ventral view.
Fig. 10. Tibia and tarsus of left male palp, retrolateral view.
Fig. 11. Tibia and tarsus of left male palp, dorsal view.
Fig. 12. Posterior end of abdomen of female.
Fig. 13. Epigynum from below.

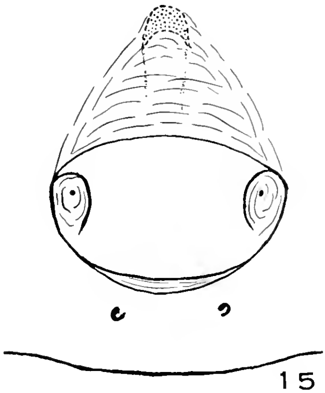
AME : ALE : PME : PLE = 5 : 10 : 6 : 8.5; AME separated from one another by 2.6 times their diameter, from ALE by nearly three times their diameter; PME separated from one another by slightly less than three times their diameter, from PLE by nearly 14/3 of their diameter; laterals separated by 2.2 times the diameter of ALE. Clypeus: strongly porrect; height, including membranous ventral border, equal to slightly more than six times the diameter of AME. Legs: 1243. Abdomen: with a short posterodorsal tubercle (Fig. 12); with the usual supply of slender spines each arising from a minute tubercle. Epigynum: quite distinctive; with a short, median scape; essentials shown in Figure 13; dissection reveals a pair of conspicuously coiled spermathecae not seen in external appearance. Color in alcohol: generally much lighter than in male; first and second legs yellowish with many reddish brown, irregular spots; first and second femora with prolateral surfaces conspicuously reddish brown with many fine, black dots each associated with a stiff bristle or spine; third and fourth legs much lighter; abdomen yellowish brown dorsally with lighter spots and narrow stripes, with alternating light and darker lateral stripes, ventrally with a broad, dark brown, median stripe.

Type locality. Male holotype and female paratype from Gamboa, Panama Canal Zone, July, 1954. Paratypes of both sexes collected at the following localities in the Canal Zone: Summit, August, 1950; Summit Gardens, August and July, 1954; Gamboa, July and August, 1954 and January, 1958; Corozal, July, 1954 and December, 1957; Balboa, May, 1964.

TMARUS IMPEDUS sp. nov.
Figures 14–15

The name of the species is an arbitrary combination of letters.

Female holotype. Total length, including the somewhat porrect chelicerae, 6.11 mm. Carapace 2.41 mm long; 2.34 mm wide opposite posterior border of second coxae where it is widest; 0.72 mm tall and, therefore, only one-third as tall as wide; ventral margin regularly rounded from opposite PLE to posterior border; other features as usual in females of the genus from Panama. Eyes: viewed from above, posterior row moderately recurved, anterior row slightly so; viewed from in front, anterior row nearly straight, measured by centers; central ocular quadrangle wider behind than in front in ratio of 4 : 3, wider behind than long in ratio of about 10 : 9. Ratio of eyes AME : ALE : PME : PLE = 5 : 12 : 7 : 12. AME separated from one another by 3.6 times their diameter, from ALE by nearly four times their diameter; PME separated from one another by nearly four times their diameter, from PLE by nearly five times their diameter; laterals separated by slightly more than 2.5 times their diameter. Clypeus quite porrect; height, including membranous ventral border, nearly equal to 8.5 times the diameter of AME; with the usual slender spines. Chelicerae, maxillae, and lip, all essentially typical of females of the genus from Panama. Sternum: scutiform; moderately convex; longer than wide in ratio of 5 : 4; widest between second coxae; with many bristles; not extended between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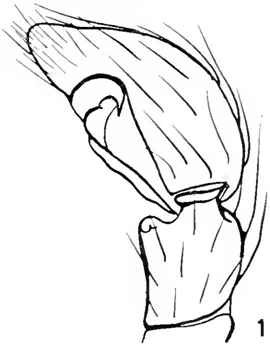
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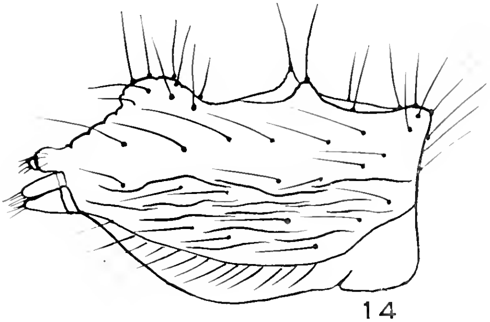
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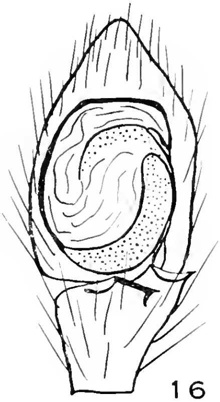
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Tmarus impedus sp. nov.

Fig. 14. Abdomen of female, lateral view, right side.
Fig. 15. Epigynum, from below.

Tmarus innotus sp. nov.

Fig. 16. Tibia and tarsus of left male palp, ventral view.
Fig. 17. Tibia and tarsus of left male palp, retrolateral view.

fourth coxae which are separated by slightly more than half their width. Legs: 1243; with numerous spines. Abdomen: very spiny; anterior, dorsal border slightly raised; slightly anterior to middle of dorsum a pair of small, conical tubercles arise, each topped by a fairly robust spine; a little behind the middle of the dorsum is a low tubercle bearing numerous spines (Fig. 14). Epigynum: somewhat distinctive (Fig. 15). Color in alcohol: the carapace has a triangular area which is yellow or whitish with small, irregular, light, reddish brown dots and spots extending from PLE to the top of the posterior declivity; from the top of the declivity a series of radiating, irregular, whitish lines extend downward over a yellowish brown background; legs yellowish with many reddish spots; prolateral surfaces of first two pairs of femora mottled with white spots; mouth parts yellowish; sternum light yellowish; abdomen with dorsum and dorsolateral sides a conglomerate of reddish spots together with irregular, whitish spots, streaks, and numerous black dots; the pair of small dorsal tubercles are largely black; venter with a median, light brownish stripe flanked on each side by an irregularly dotted white area. It seems probable that there would be much variation in the color pattern of a large population of the species.

Type locality. The holotype female is from Summit, Panama Canal Zone, August, 1950. No paratypes have appeared in my collection and the male is unknown.

TMARUS INEPTUS O. P.-Cambridge

Tmarus ineptus O. P.-Cambridge, 1892, Arachnida-Araneida, 1: 94, pl. 13, fig. 3. The holotype female is in the British Museum (Natural History). F. P.-Cambridge, 1900; Chickering, 1950; Roewer, 1954; Bonnet, 1959.

The specimens which I have assigned to this species appear to represent the most abundant of all of the species now known from Panama. I have it from many localities in the Panama Canal Zone and in Panama proper. The P.-Cambridges had the species only from Bugaba, Panama. A comparison of the figures published by the two P.-Cambridges, together with an examination of the single female on loan from the British Museum (Natural History) and the specimens in my own collection, poses serious questions regarding my previous treatment of the species. The two P.-Cambridges represented the epigynum quite differently in their respective illustrations. It now seems quite possible that it will be necessary to recognize the species in my collection as a new species. Until I have an opportunity to study all of the specimens now in the

P.-Cambridge collection and, if possible, to collect in the vicinity of Bugaba I do not think it advisable to take a more positive stand in regard to the matter.

TMARUS INNOTUS sp. nov.
Figures 16–17

The name of the species is an arbitrary combination of letters.

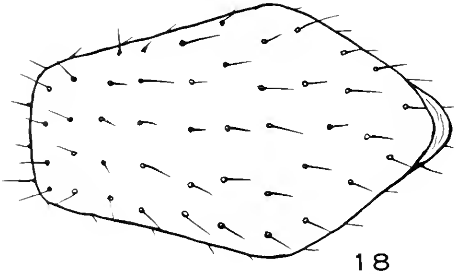
Male holotype. Total length, including somewhat porrect chelicerae, 2.8 mm. Carapace 1.1 mm long; 1.08 mm wide; 0.54 mm tall. Eyes: viewed from above, posterior row quite strongly recurved, anterior row moderately so; viewed from in front, anterior row slightly procurved, measured by centers; central ocular quadrangle wider behind than in front in ratio of 26 : 17, wider behind than long in ratio of 13 : 12; posterior row occupies about seven-tenths of width of carapace. Ratio of eyes AME : ALE : PME : PLE = 4 : 8 : 5 : 8. AME separated from one another by 2.5 times their diameter, from ALE by 2.75 times their diameter; PME separated from one another by 3 times their diameter, from PLE by slightly more than this; laterals separated by 2.25 times their diameter. Clypeus: with a long, slender spine on each side beneath interval separating AME from ALE; height equal to 4 times the diameter of AME (membranous ventral border not included). Chelicerae, maxillae, lip and sternum all essentially typical of males of the genus from Panama. Legs: 1243. Palp: exposed parts much simpler than usual in the genus from Panama; tibial apophyses unlike others seen by me; distinguishing features shown in Figures 16–17. Abdomen: a little more than twice as long as wide; posterior end somewhat extended; with a small but distinct dorsal tubercle probably indicating that the female has a well developed posterodorsal tubercle extending above the spinnerets. Color in alcohol: lateral sides of carapace a mottled, medium reddish brown; clypeus and ocular region yellowish with numerous light brown spots; dorsal area of carapace with a somewhat triangular, yellowish area with apex extending just over the top of the posterior declivity and including brownish spots of different sizes and form; mouth parts and sternum yellowish with variations. First and second femora with irregular, whitish spots on prolateral surfaces; first and second metatarsi reddish. Abdomen with an irregular whitish stripe in middorsal region; remainder of dorsum and lateral regions yellowish with minute reddish dots at bases of numerous spines; venter yellowish white.

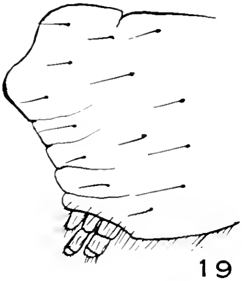
Type locality. Male holotype from Barro Colorado Island, Panama Canal Zone, July 30, 1954. There are no paratypes and the female is unknown.

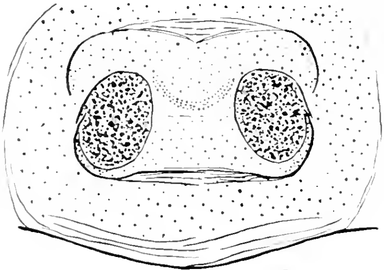
TMARUS INNUMUS sp. nov.
Figures 18–20

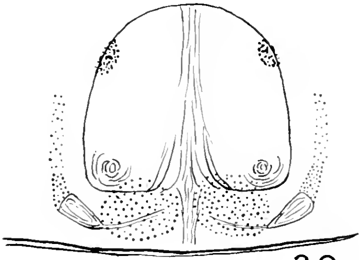
The name of the species is an arbitrary combination of letters.

Female holotype. Total length, including slightly porrect chelicerae, 9.95 mm. Carapace 3.25 mm long, 2.89 mm wide, 1.37 mm tall. Eyes: viewed from above, posterior row moderately recurved, anterior row slightly so; viewed from in front, anterior row nearly straight, measured by centers; central ocular quadrangle wider behind than in front in ratio of about 4 : 3; wider behind than long in the same ratio. Ratio of eyes AME : ALE : PME : PLE = 8 : 16 : 9.5 : 14. AME separated from one another by four times









Tmarus innumus sp. nov.

Fig. 18. Abdomen of female, dorsal view.

Fig. 19. Posterior end of abdomen of female, lateral view, right side.

Fig. 20. Epigynum, seen from below.

Tmarus levii sp. nov.

Fig. 21. Epigynum, seen from below.

their diameter; from ALE by slightly less than this. PME separated from one another by about five times their diameter; from PLE by nearly six times their diameter. Laterals separated by twice the diameter of ALE. Clypeus: moderately porrect; height, including membranous ventral border, equal to nearly nine times the diameter of AME. Chelicerae, maxillae, and lip all essentially typical of females of the genus from Panama. Sternum: typical of females of the genus from Panama; not extended between fourth coxae which are separated by two-fifths of their width. Legs: 2143; spines on first and second metatarsi shorter, more robust, and more numerous than usual in females from Panama. Epigynum somewhat distinctive as shown in Figure 20. Carapace brownish with three pairs of narrow stripes radiating over lateral sides; posterior declivity yellowish at top but dark brown elsewhere; a small brown circular area surrounds each PME. Sternum light brown. Legs yellowish with many black or gray dots and spots; first and second femora conspicuously dotted with black on prolateral and ventral surfaces; first patellae nearly black ventrally. Abdomen conspicuously chalky white dorsally with irregular, blackish bars and spots in posterior half; lateral sides irregularly white with brown spots and irregular oblique rows of black dots and short bars; venter with a light brown, median stripe flanked on each side by a row of brownish dots.

Type locality. Female holotype from Summit Gardens, Panama Canal Zone, July 19, 1954; one female paratype from Summit, C. Z., July 21, 1950. Epigynum of paratype slightly different from that of the holotype but not significantly so in my judgment. The male is unknown.

TMARUS INTENTUS O. P.-Cambridge

Tmarus intentus O. P.-Cambridge, 1892, Arachnida-Araneida, 1: 96, pl. 13, fig. 1. The holotype male from Guatemala and the female from Bugaba, Panama, are in the British Museum (Natural History). F. P.-Cambridge, 1900; Chickering, 1950; Roewer, 1954; Bonnet, 1959.

This appears to be a rare species in regions where I have collected. It has not appeared in my collections since 1936 when I took two females on Barro Colorado Island in July. Some uncertainties appear to exist in respect to this species, however. Two females on loan from the British Museum (Natural History) differ quite markedly in general appearance although the epigyna are closely similar. I hope to be able to study all specimens regarded by the P.-Cambridges as belonging to this species and, if possible, to collect in regions from which the species has been reported.

TMARUS LEVII sp. nov.
Figure 21

This species is named after Dr. Herbert W. Levi, Associate Curator of Arachnology, Museum of Comparative Zoology, Harvard University.

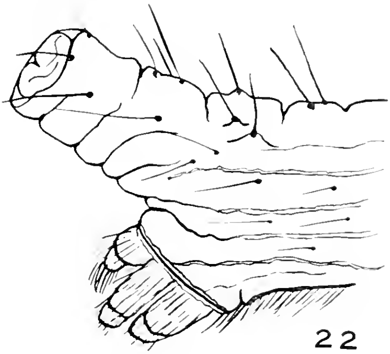
Female holotype. Total length, including bases of chelicerae, 6.37 mm. Carapace 2.4 mm long; 2.05 mm wide; about 0.98 mm tall; without a distinct thoracic groove; with numerous minute tubercles each with a long, slender spine. Eyes: viewed from above, posterior row moderately recurved, anterior row only slightly so; viewed from in front, anterior row slightly procurved, measured by centers. Central ocular quadrangle wider behind than in front in ratio of 25 : 18; wider behind than long in nearly the same ratio. Ratio of eyes AME : ALE : PME : PLE = 7 : 10.5 : 6.5 : 10. AME separated from one another by about 3.5 times their diameter, from ALE by about three times their diameter. PME separated from one another by nearly six times their diameter, from PLE by slightly less. Laterals separated by about three times the diameter of PLE. Clypeus: with a row of six spines along ventral border and with numerous bristles turned toward the middle line; height equal to nearly eight times the diameter of AME, including ventral membranous border. Chelicerae, maxillae, and lip all essentially typical of females of the genus from Panama. Sternum not extended between fourth coxae which are separated by slightly less than one-third of their width. Legs: 1243; spines essentially as usual in females of the genus from Panama; trichobothria observed on tibiae, metatarsi, tarsi and also on palpal tibiae. Abdomen: anterior border with a row of slender spines; dorsal surface with many slender spines, all apparently erectile. Distinctive features of epigynum shown in Figure 21. Carapace yellowish with light brown stripes radiating irregularly from region just above beginning of posterior declivity together with numerous brownish streaks and spots; posterior declivity light brownish with nearly white, irregular border. Clypeus yellowish with many reddish brown dots. Sternum, lip and maxillae all yellowish. Legs yellowish with many reddish dots at bases of spines; first and second femora conspicuously dotted with red on a white background along prolateral surfaces. Abdomen: dorsum whitish with many fine, dark dots and many larger, reddish dots at bases of spines; venter whitish along a broad, central stripe and darker laterally with conspicuous, narrow grooves and semitransparent dots.

Type locality. Female holotype from Barro Colorado Island, Panama Canal Zone, June, 1950. There are no paratypes and the male is unknown.

TMARUS LONGUS sp. nov.
Figures 22–23

The name of the species is a Latin adjective meaning extended, suggested by the conspicuous posterior extension of the abdomen.

Female holotype. Total length 5.33, including somewhat porrect chelicerae. Carapace 1.67 mm long; 1.36 mm wide; 0.64 mm tall. Eyes: viewed from above, posterior row moderately recurved, anterior row slightly so; viewed from in front, anterior row slightly recurved, measured by centers; central ocular quadrangle wider behind than in front in ratio of 5 : 3, wider behind than long in ratio of 15 : 14; posterior row occupies about two-thirds of width of carapace at that level. Ratio of eyes AME : ALE : PME : PLE = 4 : 11 : 5.5 : 10. AME separated from one another by slightly less than three times their diameter, from ALE by slightly less than four times their diameter; PME separated from one another by nearly 3.5 times their diameter, from PLE by nearly five times their diameter; laterals separated by nearly twice the diameter of ALE. Clypeus: moderately porrect; with a row of seven spines near ventral margin with the second from each end being very long; height equal to about 7.5 times the diameter of AME. Chelicerae, maxillae, and lip essentially typical of females of the genus from Panama. Sternum quite convex; with many long, stiff bristles; not



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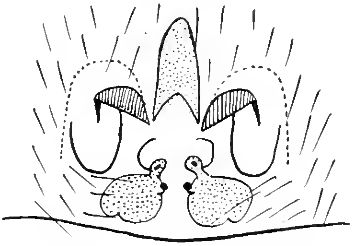

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Tmarus longus sp. nov.

Fig. 22. Posterior end of abdomen, lateral view, right side.

Fig. 23. Epigynum, seen from below.

extended between fourth coxae which are separated by five-thirteenths of their width. Legs: 1243; first two pairs of legs unusually long; spines are few in number and less conspicuous than usual in the genus from Panama. Abdomen long and slender; posterior end conspicuously extended (Fig. 22); with many spines. Epigynum complicated; with some parts quite obscure; unlike any other seen by the author (Fig. 23). Carapace with a somewhat triangular, yellowish area extending from PLE to top of posterior declivity which has a narrow white boundary and an incomplete, white, longitudinal line through the middle; dorsolateral sides light brownish with white lines and streaks extending ventrally in somewhat radiate fashion; a fairly broad, white, longitudinal band extends along lateral sides; ocular area whitish with a pair of short, yellowish, longitudinal stripes between PME. Palps and chelicerae a mixture of yellowish and white; other mouth parts yellowish. First two pairs of legs whitish with brown dots and larger spots, the latter concentrated along prolateral surfaces of first two pairs of femora; third and fourth legs yellowish with few reddish brown dots and larger spots. Abdomen: with a fairly well defined folium bounded laterally by an irregular, narrow, brown stripe extending through about three-fourths of length of abdomen; lateral and ventrolateral sides yellowish white with several narrow, longitudinal folds; venter yellowish with a narrow, irregular, whitish, ventrolateral border on each side.

Type locality. Holotype female from Panama Canal Zone Forest Preserve, Panama Canal Zone, July, 1954; one immature paratype taken in the same locality, January, 1958; the male is unknown.

TMARUS MOROSUS Chickering

Tmarus morosus Chickering, 1950, Bull. Mus. Comp. Zool., 103(4): 235, figs. 13–15. The male holotype and the female paratype are in the Museum of Comparative Zoology. Roewer, 1954: Bonnet, 1959.

The holotype is from Barro Colorado Island, Panama Canal Zone; the female paratype is from the Madden Dam region, C. Z.; paratypes are in the collection from Barro Colorado Island, C. Z. Forest Preserve, Summit Gardens, Fort Sherman, and Chilibre, all in the Canal Zone.

TMARUS MUNDULUS O. P.-Cambridge

Tmarus mundulus O. P.-Cambridge, 1892, Arachnida-Araneida, 1: 95, pl. 12, fig. 11. The holotype female from Bugaba, Panama, is in the British Museum (Natural History). F. P.-Cambridge, 1900; Chickering, 1950; Roewer, 1954; Bonnet, 1959.

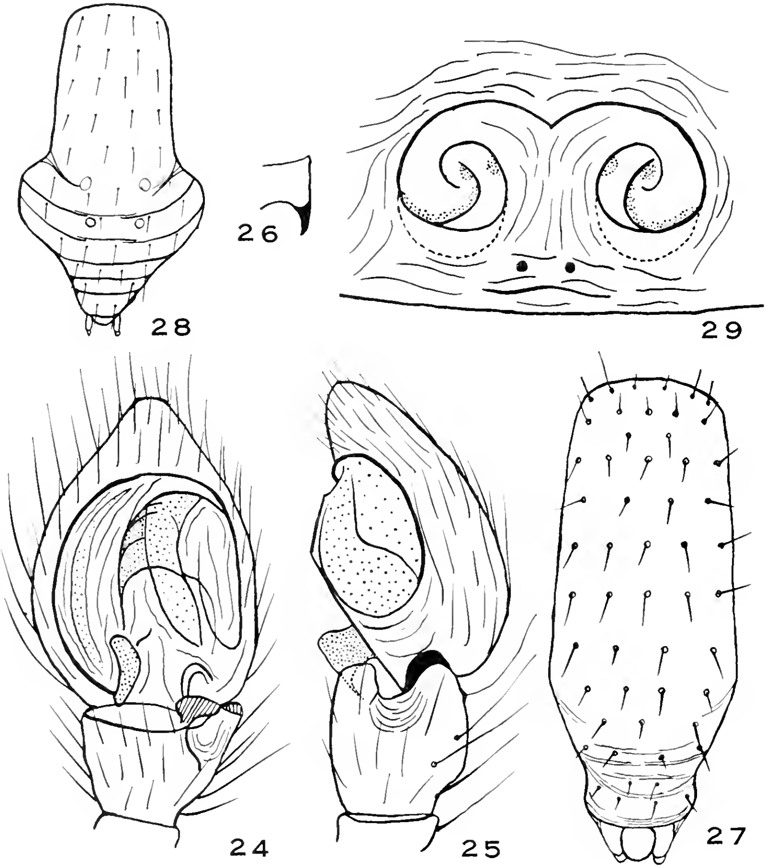
The P.-Cambridges had only females. What are believed to be both sexes have appeared in my collection in large numbers from many localities in the Canal Zone.

TMARUS OBSECUS sp. nov.

Figures 24–29

In spite of some lingering uncertainties it is regarded as fairly safe to match the sexes as they are presented below. The name of the species is an arbitrary combination of letters.

Male holotype. Total length, including bases of chelicerae, 4.49 mm. Carapace: 1.54 mm long; 1.32 mm wide; 0.57 mm tall. Eyes: viewed from above, posterior row rather strongly recurved, anterior row moderately so, not including strongly convex lenses; viewed from in front, anterior row very slightly procurved, measured by centers. Central ocular quadrangle wider behind than in front in ratio of 30 : 21; wider behind than long in ratio of 15 : 13. PLE extend somewhat beyond lateral margins of carapace at their level. Ratio of eyes AME : ALE : PME : PLE = 6 : 11 : 5 : 9. AME separated from one another by 11/6 of their diameter, from ALE by 7/3 of their diameter. PME separated from one another by four times their diameter, from PLE by slightly more than five times their diameter. Height of clypeus, including membranous ventral border, equal to 3.5 times the diameter of AME. Chelicerae, maxillae and lip typical of males of the genus in Panama. Sternum only slightly convex; posterior end bluntly pointed but not extended between fourth coxae which are separated by nearly one half their width. Legs: 1243. Palp: distinctive features shown in Figures 24–26; both tibial apophyses short, blunt. Abdomen: elongated; lateral sides nearly parallel throughout two-thirds of length and then sharply narrowed; a slight widening just before constriction is taken to indicate a tendency to inflate as in the female. Carapace with steep posterior declivity a fairly uniform brown; radiating from top of posterior declivity are several irregular, yellowish and brown stripes covering most of dorsal surface and extending laterally to make a complicated color pattern; clypeus a dark brown; anterior surface of chelicerae brownish with yellowish stripes. Sternum brown with elongated darker spots extending toward center from margin. Legs generally light brown with many irregular, reddish and yellowish spots; first femora with a dark brown stripe along prolateral surface; second femora with a similar stripe but much broken into separate spots; third and fourth legs much lighter. Abdomen: dorsum brownish in general but this results from a conglomeration of brown streaks and spots on a light yellowish background; a median lighter streak extends through the entire length of the dorsum; lateral sides with narrow rows of elongated, brown spots and streaks alternating with yellowish streaks; venter with a broad, brownish, median, longitudinal stripe flanked on each side by a narrower yellowish stripe.



Tmarus obsecus sp. nov.

Fig. 24. Tibia and tarsus of left male palp, ventral view.
Fig. 25. Tibia and tarsus of left male palp, retrolateral view.
Fig. 26. Basal, palpal, tarsal apophysis, prolateral view.
Fig. 27. Abdomen of male, dorsal view.
Fig. 28. Abdomen of female, dorsal view.
Fig. 29. Epigynum, seen from below.

Female paratype. Total length, including somewhat extended chelicerae, 8.13 mm. Carapace 2.47 mm long; 2.2 mm wide; about 0.98 mm tall. Eyes: viewed from above, posterior row moderately recurved, anterior row slightly so; viewed from in front, anterior row straight, measured by centers. Central ocular quadrangle wider behind than in front in ratio of about 3 : 2; wider behind than long in about the same ratio. Ratio of eyes AME : ALE : PME : PLE = 6 : 13 : 8 : 11. AME separated from one another by slightly more than three times their diameter, from ALE by about 3.5 times their diameter. PME separated from one another by slightly more than four times their diameter, from PLE by about 4.75 times their diameter. Laterals separated by nearly twice the diameter of PLE. Clypeus quite porrect; ventral margin with numerous spines (some indicated only by scars); height, including membranous ventral border, equal to slightly more than six times the diameter of AME. Chelicerae, maxillae and lip typical of females of the genus from Panama. Sternum moderately convex; not extended between fourth coxae which are separated by a little more than one-sixth of their width. Legs: 1243. Abdomen: inflated laterally in posterior half as shown in Figure 28. Carapace reddish brown with several narrow, yellowish lines and reddish brown bands radiating from top of posterior declivity; lateral sides irregularly spotted with reddish brown on a yellowish background; steep posterior declivity nearly all reddish brown. Chelicerae brownish with a yellowish stripe along median boundary. Lip brown, lighter at distal end. Maxillae yellowish in general but brownish in median halves. Sternum brown. First and second legs brownish in general with irregular yellowish spots; femora of these legs with a broad, brown, prolateral stripe throughout; third and fourth legs much lighter with the femora also with a broad, prolateral stripe much lighter in color. Abdomen: dorsum dark colored with many small, red dots and larger reddish spots; extending through the middle of the anterior half of the dorsum is a narrow, irregular, dark stripe fringed with yellow; this is continued to the anal tubercle by a broken, median yellow stripe; the inflated region has a broken, yellow bar extending across and down the lateral sides; lateral sides with a series of narrow, alternating, black and reddish, longitudinal stripes; venter with a fairly broad, median, longitudinal, light brown stripe flanked on each side by a broader, yellow stripe with dark, irregular dots.

Type locality. Male holotype from Summit, Panama Canal Zone, August, 1950; female paratype from Barro Colorado Island, C. Z., January, 1958; one immature female paratype from Summit, C. Z., November, 1946 (N. L. H. Kraus).

TMARUS PARKI Chickering

Tmarus parki Chickering, 1950, Bull. Mus. Comp. Zool., 103(4): 242, figs. 19–20. The male holotype from Barro Colorado Island, Panama Canal Zone, is in the Museum of Comparative Zoology. Roewer, 1954; Bonnet, 1959.

One additional male of this species was taken on Barro Colorado Island, C. Z., January, 1958. This specimen has a much brighter color pattern than was shown by the holotype; the carapace is brightly colored somewhat like that of *T. decorus* sp. nov.; the dorsum of the abdomen has each spine arising from a red dot surrounded by a yellowish ring. The female is unknown.

TMARUS PAUPER O. P.-Cambridge

Tmarus pauper O. P.-Cambridge, 1892, Arachnida-Araneida, 1: 96, pl. 12, fig. 8. The male holotype is in the British Museum (Natural History). F. P.-Cambridge, 1900; Chickering, 1950; Roewer, 1954; Bonnet, 1959.

The P.-Cambridges had only the male from Bugaba, Panama. The species has not yet appeared in my collections and, so far as I know, has not been reported since the original collections were made.

TMARUS PEREGRINUS Chickering

Tmarus peregrinus Chickering, 1950, Bull. Mus. Comp. Zool., 103(4): 245, figs. 21–22. The male holotype is in the Museum of Comparative Zoology. Roewer, 1954; Bonnet, 1959.

The male holotype was taken on Barro Colorado Island, Panama Canal Zone, July, 1934 and has not appeared in my collections since that time. The female is unknown.

TMARUS PROBUS Chickering

Tmarus probus Chickering, 1950, Bull. Mus. Comp. Zool., 103(4): 247, figs. 23–24. The male holotype together with several paratype males from several different localities in the Panama Canal Zone and Panama proper are in the Museum of Comparative Zoology. Roewer, 1954; Bonnet, 1959.

The species has been collected on four different dates since the publication of my paper in 1950, and all within the Canal Zone. Dr. James Zetek contributed a specimen taken in El Cermeno, Panama, January, 1940.

TMARUS PRODUCTUS Chickering

Tmarus productus Chickering, 1950, Bull. Mus. Comp. Zool., 103(4): 249, figs. 25–26. The male holotype from Porto Bello, Panama, is in the Museum of Comparative Zoology. Roewer, 1954; Bonnet, 1959.

The species has appeared in my collections only twice in recent years: Summit, July, 1950, and Summit Gardens, July, 1954, Panama Canal Zone. It seems possible that the female *T. impedus* sp. nov. is the missing female for this species.

TMARUS PROTOBIUS sp. nov.

Figure 30

The name for this species is an arbitrary combination of letters.

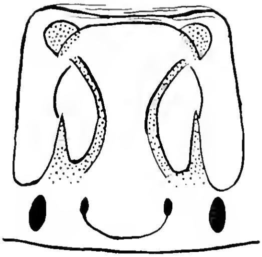
Female holotype. Total length 5.46 mm, including somewhat porrect chelicerae. Carapace 1.65 mm long; 1.36 mm wide; 0.77 mm tall. Eyes: viewed from above, posterior row rather strongly recurved, anterior row moderately so, exclusive of the very convex lenses of ALE; viewed from in front, anterior row gently procurved, measured by centers. Central ocular quadrangle wider behind than in front in ratio of 29 : 19; slightly wider than long. Ratio of eyes AME : ALE : PME : PLE = 4.5 : 11.5 : 7 : 10.5. AME separated from one another by slightly more than twice their diameter, from ALE by a little more than three times their diameter. PME separated from one another by about 2.5 times their diameter, from PLE by a little more than 3.5 times their diameter. Laterals separated by twice the diameter of PLE. Clypeus: moderately porrect; height, including membranous ventral border, nearly six times the diameter of AME. Chelicerae, maxillae, and lip essentially typical of females of the genus from Panama. Sternum: moderately convex; posterior end sharply pointed, not extended between fourth coxae which are separated by five-thirteenths of their width. Legs: 1243. Abdomen: with a well defined posterodorsal tubercle. Epigynum: somewhat distinctive (Fig. 30); quite unlike that seen in any other species known to me. Carapace in general light yellowish but with irregular, brownish lines radiating from a central light colored region out over dorsolateral sides; posterior declivity light brownish in center and light yellowish on lateral sides. Chelicerae: each with a narrow, light yellowish, lateral stripe and with anterior surface a mixture of irregular light lines and light brownish spots. Other mouth parts yellowish. Sternum: yellowish with an irregular row of red dots along each lateral region. Legs: in general yellowish with many reddish dots, white spots and streaks; first femora with an irregular, prolateral, brown stripe with red dots and streaks along margins; second femora with a whitish, prolateral stripe and many red dots; ventral surfaces of segments from patellae to tarsi are similarly but less conspicuously colored. Abdomen: with a dorsal, light brownish folium bordered by narrow, white lines; lateral sides whitish with fine dots arranged in irregular, longitudinal lines; ventrolaterally there is a series of light brownish, irregular, narrow stripes; venter light yellowish with a pair of dotted lines close to midventral region and a single dotted line on each side near the lateral border.

Type locality. Holotype female from Barro Colorado Island, Panama Canal Zone, August, 1950. One paratype female from Summit Gardens, C. Z., July, 1954. The male is unknown.

TMARUS RUBINUS sp. nov.
Figures 31–32

The name of the species is an arbitrary combination of letters.

Female holotype. Total length, including somewhat porrect chelicerae, 6.11 mm. Carapace 1.96 mm long; 1.69 mm wide; about 0.98 mm tall. Eyes: viewed from above, posterior row moderately recurved, anterior row gently so; viewed from in front, anterior row probably straight (raised cuticle makes it difficult to measure accurately). Central ocular quadrangle wider behind than in front in ratio of about 3 : 2; wider behind than long in ratio of about 4 : 3. Posterior row of eyes occupies about five-sixths of width of carapace. Ratio of eyes AME : ALE : PME : PLE = 5.5 : 12.5 : 7.5 : 10. AME separated from one another by slightly more than three times their diameter, from ALE by about the same distance. PME separated from one another by slightly less than four times their diameter, from PLE by about the same distance. Laterals separated by 1.8 times the diameter of PLE. Clypeus moderately porrect; height equal to about six times the diameter of AME. Chelicerae, maxillae, and lip essentially typical of females of the genus from Panama. Sternum: only slightly convex; not extended between fourth coxae which are separated only by about one-fifth of their width. Legs: 1 = 234. Abdomen: with posterodorsal tubercle quite conspicuously developed (Fig. 31); otherwise essentially typical of females of the genus from Panama. Epigynum: obscurely distinctive; essentials shown in Figure 32. Carapace light brownish in general with whitish spots and streaks; dorsal radiations, so conspicuous in several species, are here obscure and poorly defined; posterior declivity with a whitish spot



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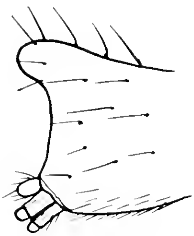

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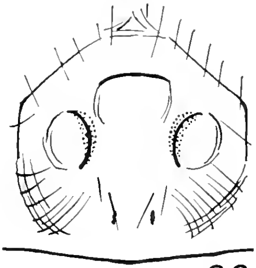

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Tmarus protobius sp. nov.

Fig. 30. Epigynum, seen from below.

Tmarus rubinus sp. nov.

Fig. 31. Posterior end of abdomen of female, lateral view, right side.
Fig. 32. Epigynum, seen from below.

at top with remainder a variable brownish. Sternum light yellowish. Legs: yellowish in general with many small, reddish brown spots; first two pairs of femora conspicuously mottled with reddish brown along the whole prolateral surface; dorsal and lateral surfaces of abdomen light yellowish with many small, reddish and whitish dots, irregular spots and streaks; venter with a broad, unicolorous, yellowish, median stripe; lateral sides of the median stripe irregularly whitish.

Type locality. Female holotype from Summit Gardens, Panama Canal Zone, July, 1954. There are no paratypes and the male is unknown.

TMARUS SIGILLATUS Chickering

Tmarus sigillatus Chickering, 1950, Bull. Mus. Comp. Zool., 103(4): 252, figs. 27–28. The male holotype from the Panama Canal Zone Forest Preserve, C. Z., is in the Museum of Comparative Zoology. Roewer, 1954; Bonnet, 1959.

Several males have been added to the collection from Summit, C. Z. Forest Preserve, and Summit Gardens, all in the Canal Zone and all taken during the past fourteen years. The female remains unknown.

TMARUS STUDIOSUS O. P.-Cambridge

Tmarus studiosus O. P.-Cambridge, 1892, Arachnida-Araneida, 1:97, pl. 12, fig. 6. Types of both sexes are in the British Museum (Natural History), from Bugaba, Panama. F. P.-Cambridge, 1900; Chickering, 1950; Roewer, 1954; Bonnet, 1959.

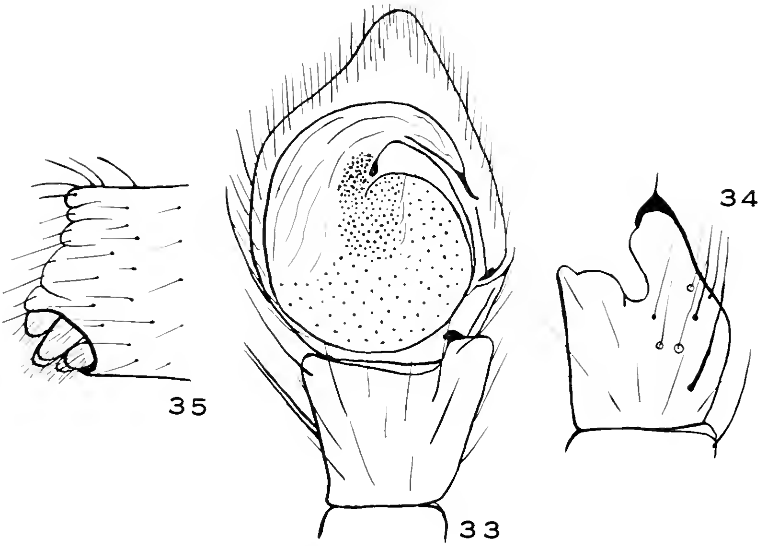
The collection now includes both sexes of this species from many localities in the Canal Zone where it appears to be abundant.

Tmarus vitusus sp. nov.

Figures 33–35

The name of the species is an arbitrary combination of letters.

Male holotype. Total length 4.68 mm. Carapace 1.76 mm long; 1.69 mm wide; about 0.68 mm tall. Eyes: viewed from above, posterior row quite strongly recurved, anterior row gently so (exclusive of very convex lenses of ALE); viewed from in front, anterior row almost straight, measured by centers. Central ocular quadrangle wider behind than in front in ratio of 10 : 7; wider behind than long in ratio of 5 : 4. Posterior row of eyes occupies nearly full width of carapace. Ratio of eyes AME : ALE : PME : PLE = 5 : 11 : 7 : 10. AME separated from one another by 3.6 times their diameter, from ALE by three times their diameter. PME separated from one another by 3.7 times their diameter, from PLE by slightly more than 4.4 times their diameter. Laterals



Tmarus vitusus sp. nov.

Fig. 33. Left palp of male, ventral view.
Fig. 34. Left palpal tibia, retrolateral view.
Fig. 35. Posterior end of abdomen, lateral view.

separated by 2.5 times the diameter of PLE. Clypeus: with a row of six long, slender spines near ventral border and a single similar, medial spine below the interval separating AME. Chelicerae, maxillae, and lip essentially typical of males of the genus from Panama. Sternum moderately convex; squarely terminated halfway between fourth coxae which are separated by slightly more than half their width. Legs: 1243. Palp: essential features shown in Figures 33–34. Abdomen: with a small but definite posterodorsal tubercle (Fig. 35), probably indicative of a more or less prominent tubercle in the female of the species. Carapace with a nearly triangular area outlined in yellowish enclosing a brownish region just behind PME; just posterior to the apex of this region is a somewhat rounded, yellowish area reaching a short distance down the posterior declivity; remainder of dorsal region, posterior declivity and lateral sides are a mottled yellowish and brownish color; interocular and clypeal region a dotted, yellowish coloration. Legs yellowish with many brown dots, especially marked on prolateral surfaces of femora, patellae, and tibiae of first and second legs. Sternum yellowish with fine, brown, irregular dots. Abdomen: dorsal and lateral sides in general grayish with a darker median streak extending through anterior half and four narrow, darker, cross bars poorly outlined; venter with a rounded, brownish spot in front of genital groove and a median, longitudinal, light brown stripe bordered by very light areas and extending nearly to the spinnerets.

Type locality. Male holotype from Gamboa, Panama Canal Zone, July 24, 1954. There are no paratypes and the female is unknown.

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Bulletin of the Museum of Comparative Zoology
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THE RELATIONSHIPS OF FOUR SMALL HISPANIOLAN *ELEUTHERODACTYLUS* (LEPTODACTYLIDAE)

By Albert Schwartz

CAMBRIDGE, MASS., U.S.A.
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No. 8 — *The Relationships Of Four Small Hispaniolan* Eleutherodactylus (*Leptodactylidae*)

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Perhaps the most confusing group of the genus *Eleutherodactylus* in the West Indies is that composed of the small to minute frogs of Hispaniola, none of which has a snout-vent length in excess of 25 mm. To this assemblage belong *E. minutus* Noble 1923, *E. abbotti* Cochran 1923, *E. audanti* Cochran 1934, and *E. haitianus* Barbour 1942 (= *E. intermedius* Cochran 1941, preoccupied). *E. abbotti* was described from Laguna, Samaná Province, República Dominicana, *E. audanti* from Peak la Selle (= Mont la Selle), Dept. de l'Ouest, Haiti. The remaining two forms were described from the interior uplands of the Cordillera Central in La Vega Province (República Dominicana), *minutus* from near Paso Bajito, Jarabacoa-Constanza Trail, and *haitianus* from Loma Rucilla, 8000 to 10,000 feet. Although *minutus* and *haitianus* are still known only from various localities in the Cordillera, *abbotti* has been reported from many localities in the República Dominicana and Haiti. *E. audanti* is here reported for the first time from outside of the Massif de la Selle.

Shreve and Williams (1963: 320–323) discussed at some length the situation of the species *audanti* and *abbotti* in the Port-au-Prince region. Conclusions drawn from my own experience in the field in both Haiti and the República Dominicana in 1962 and 1963 differ from theirs, and are drawn in part from a large body of fresh material from critical localities both outside and within the range of their particular study.

Through the courtesy and cooperation of the following curators, I have been able to study specimens of this group of frogs: Ernest E. Williams, Museum of Comparative Zoology (MCZ); Doris M. Cochran, United States National Museum (USNM); and Charles M. Bogert and Margaret Bullitt, American Museum of Natural History (AMNH). Specimens in my own collection are designated Albert Schwartz Field Series (ASFS). In the field in Hispaniola I had the capable assistance of Patricia A. Heinlein and Ronald F. Klinikowski, Dennis R. Paulson, David C. Leber, and Richard Thomas. To all of them I express my sincere thanks for their interest in these small frogs. The illustrations for the present paper are the work of Klinikowski and Leber; they again merit my gratitude for their endeavors.

ELEUTHERODACTYLUS ABBOTTI AND *ELEUTHERODACTYLUS AUDANTI* ON THE SOUTH ISLAND[1]

Although *E. abbotti* was known from the south island by only two doubtfully identified specimens (from Pétionville and Fond-des-Nègres, Haiti) at the time of Cochran's monograph on the herpetology of Hispaniola (1941), it is now known from many localities there.

Shreve and Williams (1963) in a study of a large number of small frogs from the La Selle region presented the following conclusions: 1) *audanti* is a subspecies of *abbotti* because "of the presence in the lowlands of the Port-au-Prince region and on the southwest peninsula and in Barahona of equivocal specimens which appear to be in various grades and degrees intermediate between *audanti* and *abbotti*"; 2) there are no absolute differences between these two species; 3) at intermediate levels north of the Massif de La Selle, such as Furcy, there exist populations of frogs, some of which may be identified as *abbotti*, others as *audanti*, and still others intermediate between these two species; and 4) material from various lowland and highland localities (Península de Barahona, Morne de Cayette, Pétionville, Fond-des-Nègres, Thiotte) cannot be referred with certainty to either *abbotti* or *audanti* and are considered to be intergrades. An interesting sidelight on Shreve and Williams' study was the discovery of "the presence in the foothills of the La Hotte region . . . of frogs much more like *abbotti* than any others in the area south of the Cul de Sac Plain." This analysis would suggest that *abbotti* and *audanti* are conspecific, and that *audanti* is restricted to the highest peaks of the La Selle, intergrades with *abbotti* at lower levels, and is replaced by *abbotti* in the lowlands.

However, while collecting at Furcy in the summer of 1962, it quickly became obvious that we were dealing with two types of small frogs. Both are vocally very similar; the call of each is a series of highpitched "tuck" 's, followed by a sharply ascending "wheep" (although a series of "tuck-wheep, tuck-wheep" 's may be interspersed in the normal call series, usually at its end or beginning). The call of the smaller of these two frogs (*audanti*) was distinctly higher than that of the larger (*abbotti*), but otherwise the calls were identical in structure. However, these two forms differ markedly from one another in that *abbotti* has a

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[1] The terms "south island" and "north island" are used in this paper as, for example, by Williams, 1961.

grayish green to tan ground color, is without definite leg bars and postanal triangle (Fig. 1, left), and has an all yellow venter, whereas *audanti* has a much more brightly colored dorsum, most often some shade of reddish brown or buff, with a distinct and clear-cut postanal triangle and leg bars (Fig. 1, right), and a gray belly which is often spotted.

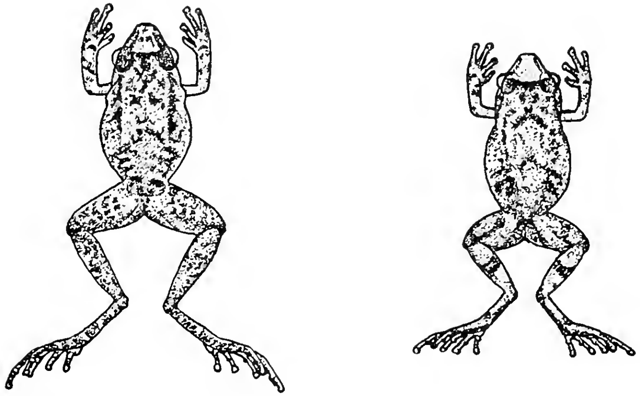

FIG. 1. *Left:* *Eleutherodactylus abbotti*, adult female, ASFS X1649, Furcy, 5600′, Dépt. de l'Ouest, Haiti; snout-vent length 23.0 mm.
Right: *Eleutherodactylus audanti audanti*, adult female, ASFS X2362, 2.4 mi. S Kenscoff, Dépt. de l'Ouest, Haiti; snout-vent length 23.3 mm.

All the preserved specimens of these frogs collected by others in the Furcy area can be separated into these two categories without difficulty. Naturally, the yellow ventral coloration is no longer present; the distinct leg and postanal markings of *audanti* remain, however, and these are a ready means of differentiation between the two species. Occasional "intermediates" (i.e., *audanti* with slightly less clear-cut postanal triangle or *abbotti* with more definite leg bands) I consider to be within the natural range of variation of each of the two species involved; the Furcy population is in no way composed of a large number of intergrades with *abbotti* and *audanti* at the two extremes. It is, rather, composed of frogs which are readily assignable to either *audanti* or *abbotti* on the basis of pattern, with a very occasional specimen of each whose markings slightly resemble those of the other species in degree of clarity. Thus, at least at Furcy, *audanti* and *abbotti* appear not as two races of one form, but as two sympatric species.

The following table (Table I) is based on a selection of ten specimens of each sex of each species (using as the criterion for species the pattern described above) from the south island Haitian uplands. These series include the largest member of each sex in each case, and the type (a female) of *audanti,* as well as three other adult female paratypes. Measurements and ratios indicate the following: in males, *abbotti* reaches a larger size than *audanti* (in females, the reverse appears to be true, but this is apparently an artifact of the *abbotti* sample, since there are female *abbotti* from medium elevations in the Cordillera Central which have a snout-vent length equal to that of the largest *audanti*); measurements of femur, tibia, and fourth toe are diagnostic, as is the tibia/snout-vent ratio.

TABLE I[1]
(measurements in millimeters)

	Snout-vent length (maximum)	Tibia		Femur		Tibia/snout-vent ratio	
		range	average	range	average	range	average
abbotti ♂	19.3	8.8–10.1	9.3	7.7– 8.5	8.0	48.6–55.4	52.2
audanti ♂	18.4	7.2– 8.0	7.6	6.1– 7.0	6.6	40.8–46.8	43.8
abbotti ♀	23.6	11.1–13.0	11.9	9.7–11.4	10.2	50.4–56.6	53.5
audanti ♀	25.3	9.0–10.8	10.1	8.0– 9.8	9.1	38.6–47.1	43.6

The following additional descriptive notes on the patterns of the two species should be helpful. *E. audanti* is well illustrated by Cochran (1941: 66). The heavily and distinctly crossbarred limbs and the dark postanal triangle are clearly shown. The leg bars — one on the crus, one on the pes, and two incomplete bars on the thigh — are usually outlined in preserved material by pale bands, which set the bars off very distinctly from the ground color. There is a single bar on the antebrachium, and another on the wrist, again outlined by pale color. The dorsal pattern may have a middorsal stripe. The major feature of the dorsal pattern is a scapular X, the anterior limbs of which are usually fused to the dark interocular bar; often the area between the interocular bar and the anterior arms of the X is likewise dark, thus giving a

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[1] Head measurements, not included in the table, are less clear-cut. In males all these measurements overlap greatly, although *abbotti* averages consistently higher. In females, *abbotti* averages larger in head length (8.2 vs. 8.1) and naris to eye (2.4 vs. 2.2), but slightly less in head width (8.4 vs. 8.5) and diameter of tympanum (1.4 vs. 1.5); diameter of eye averages the same in both species (3.0), although the eye of *abbotti* reaches a larger maximum size. In no head measurements are the females of the two species separable.

rather complex occipital and scapular figure. The sides may be dark like the back, or may have a series of about five horizontal bars before the groin. Two fresh specimens have a tan dorsal band from snout to vent, with darker brown sides, the scapular X faint but still present. The ventral dark pigmentation is variable, but always present; there may be stippling, mottling, or even blotching on the throat and belly; the underside of the hindlimbs is always heavily stippled with brown. The pale snout of *audanti* is a characteristic of the species.

E. abbotti, on the other hand, is generally paler than *audanti* when preserved, and although it has the scapular X which is joined to the interocular bar, the same number of limb bands as *audanti*, and even, at times, has the vertical side stripes, none of the features is so bold and diagrammatic as in *audanti*. The entire dorsal surface is irregularly mottled with darker color, and the individual pattern elements are lost in the general obliterative effect of the dorsal pigmentation. There is no clear-cut postanal triangle, although the postanal area is somewhat darker than the rest of the concealed surfaces. The limb bars are not set off from the ground color by a distinct pale area; in fact, they have been so much invaded by pale color that they are no longer conspicuous. Usually the ventral surfaces are almost immaculate, although there may be some diffuse stippling on the throat, and an occasional individual has some belly stippling.

Cochran (1941: 67–68) has described in great detail the pallid dorsal coloration and asymmetrical spotting which occur in some specimens of *audanti*. Apparently the entire dorsum loses its basic pattern, and a blotchy, irregular, asymmetrical pattern is superimposed upon the now unicolor back, so that the preserved specimen is pale, variously and irregularly mottled with dark brown. Of the large series from Furcy available, only two individuals show this mottling, and even in them it is apparently in its earliest stages. The back of one still retains some semblance of pattern, but there are large licheniform patches on the hindlimbs. The other is uniform pale pinkish dorsally, but the hindlegs show expansion of the dark pigment from the crural bands and elsewhere on the legs. This irregularly mottled state is more common in specimens from the high La Selle, where large numbers in any given series may be mottled. The faded back and increased mottling is not a condition of age, since some tiny juveniles, as well as adult and subadult males and females all show the mottled state. Invariably, from any single locality, there are both "normal" and mottled individuals in the sample.

Shreve and Williams (1963: 322) stated that "nothing . . . comparable to the orange or asymmetrically pigmented specimens of *audanti* occurs in the *abbotti* populations north of the Cul de Sac." However, there is a single specimen of *abbotti* from the lowlands near Pimentel in the República Dominicana (and thus well outside the range of *audanti*) which clearly shows this condition. In addition, there are frogs (for example, one from Furcy, MCZ 33549, one from Savane Zombi, MCZ 31953, and two from 10.5 miles south of Cabral, ASFS V71 and V83) which are typical *abbotti* in size, proportion, and residual pattern, and show no *audanti* influence in these respects, but which, nevertheless, have the mottled condition of *audanti*. These could, perhaps, be considered intergrades. However, there are typical *abbotti* available from the same localities, and, of the three localities, only at Furcy do the two species occur together. Since *abbotti*, when far outside *audanti* genetic influence, may manifest this sort of peculiar spotting, I regard these specimens as within the chromatic variation of *abbotti*.

Since *audanti* and *abbotti* are members of the *auriculatus* group, both have external vocal sacs, granular bellies, small patch-like vomerine teeth, and enlarged digital discs. I am unable to distinguish the two species on any structural basis; one possibility is that the vomerine teeth of *abbotti* are slightly more oblique than those of *audanti*, but this is at best a very subjective character. Like most members of the *auriculatus* group, both *audanti* and *abbotti* lack inguinal glands.

E. audanti is known from near the Dominico-Haitian border (Forêt des Pins) west to the vicinity of Pic Macaya (foothills, Massif de la Hotte). It is restricted to the uplands — the lowest locality whose altitude is known and whence *audanti* has been collected is Peneau, 5000 feet. A possibly lower locality is 2.4 miles south of Kenscoff, but no altitude is available. The highest locality is Mont Cabaio (7000 feet), although specimens are recorded from Mont la Selle, without elevation given (the summit of Mont la Selle is slightly over 8000 feet). The specimens from Pic Macaya (MCZ 21551–53) represent the only Haitian *audanti* outside of the Massif de la Selle; they do not differ in pattern from La Selle specimens. The adult female of the series has a tibia/snout-vent ratio of 48.9, slightly greater than that reported above for La Selle frogs.

In the La Selle region, *abbotti* occurs with *audanti* at elevations up to 5600 feet (Peneau, Furcy, 2.4 miles south of Kenscoff). There are specimens of *abbotti* from Savane Zombi (4200 feet) but none from Forêt des Pins at 5800 feet where *audanti* has been collected. *E. abbotti* has also been collected from the lower southern slopes of the La Selle (one specimen, Thiotte, about 3000 feet); from the northern lowlands of the eastern Tiburon Peninsula (one specimen, Morne de Cayette); from the western extremity of the Tiburon, both north (one specimen, Marfranc, 120 feet) and south (eight specimens, Camp Perrin, 1000 feet) of the Massif de la Hotte; and from the intermediate southern slopes of this range (five specimens, Carrefour Canon, 500 feet). (See Fig. 5 for distribution of these two species.)

A large amount of fresh material from the Península de Barahona and the Sierra de Baoruco indicates that *abbotti* occurs there as well. In this region it has been taken from near sea level (La Ciénaga) up to 3700 feet in the Sierra de Baoruco. In fact, *abbotti* is the dominant small frog in this entire region. The absence of *audanti* from the Sierra de Baoruco may be more apparent than real. Since *audanti* in the La Selle has not been taken lower than about 5000 feet, it may well not occur at lower elevations in the Sierra de Baoruco. Most collecting in these mountains has been in the Valle de Polo region, whose elevation is less than that for the lowest record of *audanti* to the west.

In summary, *E. abbotti* is widespread throughout the south island, occurring from about sea level to elevations of 5600 feet. The species occurs not only in the lowlands, but in the La Hotte-La Selle-Baoruco massif up to moderate elevations. *E. audanti*, on the other hand, is known only from elevations above 5000 feet in the massifs de la Hotte and la Selle, and in the latter range is extremely abundant at these higher elevations. Its occurrence on the Sierra de Baoruco requires confirmation.[1] Both species occur together at elevations between 5000 and 5600 feet, at least in the Massif de la Selle.

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[1] Since the above was written, David C. Leber and Richard Thomas, in the summer of 1964, succeeded in securing *E. audanti* in the Sierra de Baoruco. Near the Dominico-Haitian border, eleven specimens of *audanti* were secured between 4 and 11 kilometers northeast of Los Arroyos, Pedernales Province, at elevations between 5600 feet and 7200 feet. In this same general region, nine specimens of *E. abbotti* were also collected; these are from six localities ranging in elevation from 2200 feet to 5800 feet. The latter high elevation gives an increase of altitudinal overlap between *audanti* and *abbotti* of 200 feet in the southern massifs. At one locality (5 km NE Los Arroyos) both species were collected together. These new localities are not included on the map, nor are these specimens included in the computations.

ELEUTHERODACTYLUS ABBOTTI AND *ELEUTHERODACTYLUS AUDANTI* ON THE NORTH ISLAND

E. abbotti has long been known to occur throughout much of the north island. Described from Laguna on the Península de Samaná, this frog was subsequently reported from many localities in the República Dominicana (Cochran, 1941; Mertens, 1939), from the Dominico-Haitian border east to the Península de Samaná and the south shore of the Bahía de Samaná. Its distribution in Haiti is poorly known; it has been reported only from near Limbé (Lynn, 1958), the Citadelle (Cochran, 1941: 61), and Grande Rivière (Shreve and Williams, 1963: 322). The relatively small number of specimens of *abbotti* in collections prompted Shreve and Williams to suggest that *abbotti* was "nowhere very abundant." On the contrary, *abbotti* is an extremely abundant frog, somewhat more so in the uplands than in the lowlands. Not only can it be collected at night, when huge choruses make the forest resound, but can often be secured with ease during the day in piles of coconut trash and old, rotting, and very wet piles of cacao husks.

In the Cordillera Central *abbotti* occurs up to elevations of 6000 feet (Loma Vieja; 9.1 miles north of Constanza; 9.3 miles north of Constanza). In the Sierra de Neiba it occurs at elevations as high as 5000 feet (14.5 miles south of Elías Piña). The Cordillera elevation is slightly in excess of the highest known records in the Massif de la Selle, but not strikingly so. The altitude of major abundance in the Cordillera is apparently about 3600–4000 feet, where *abbotti* forms the largest portion of nocturnal frog choruses in broadleaf gallery forest along rivers in pinewoods.

The measurements of three series of *abbotti* (ten males and ten females each) from southern Haiti (La Selle), the interior Dominican uplands (Cordillera), and northern República Dominicana are tabulated below (Table II) and reveal certain differences among them. (Each series included the largest members of both sexes; in each series most females were gravid.)

In coloration and pattern there appear to be no differences among the various populations studied. The typical dorsal ground color varies from gray to some shade of tan or light brown; there is a dark interocular bar, crossbars on the limbs, a yellowish to whitish-gray belly, and a yellow vocal sac. Despite its wide geographic and altitudinal distribution, *abbotti* has apparently not differentiated into races.

TABLE II. Means and extremes of nine measurements and one ratio in three populations of *Eleutherodactylus abbotti* consisting of the ten largest specimens of each sex from each region. (No races are recognized.)

	Haitian uplands	República Dominicana uplands	northern República Dominicana
	10♂	10♂	10♂
snout-vent length	17.9 (16.4–19.3)	18.5 (17.9–18.9)	17.8 (17.0–18.8)
head length	6.5 (6.1– 7.0)	6.4 (6.0– 6.9)	6.4 (6.0– 6.8)
head width	6.6 (6.0– 7.1)	6.5 (6.3– 7.3)	6.6 (6.0– 7.4)
tympanum	1.3 (1.1– 1.4)	1.2 (1.0– 1.3)	1.2 (1.0– 1.5)
eye	2.6 (2.5– 2.7)	2.4 (2.2– 2.6)	2.7 (2.3– 3.0)
naris to eye	1.8 (1.6– 2.0)	1.9 (1.7– 2.0)	1.8 (1.7– 2.0)
femur	8.0 (7.7– 8.5)	7.7 (7.1– 8.3)	7.8 (7.5– 8.2)
tibia	9.3 (8.8–10.1)	8.8 (8.5– 9.3)	8.8 (8.5– 9.3)
fourth toe	8.3 (7.5– 9.3)	7.6 (6.6– 8.1)	7.5 (7.0– 7.8)
tibia/snout-vent ratio	43.8 (40.8–46.8)	47.9 (45.5–51.1)	50.0 (45.7–52.5)
	10♀	10♀	10♀
snout-vent length	22.2 (20.9–23.6)	22.7 (20.4–25.4)	21.4 (20.9–22.8)
head length	8.2 (7.4– 9.3)	8.1 (7.1– 8.8)	7.8 (7.5– 8.4)
head width	8.4 (7.9– 9.2)	8.1 (6.9– 9.6)	7.9 (7.5– 8.7)
tympanum	1.4 (1.3– 1.6)	1.5 (1.2– 1.7)	1.4 (1.2– 1.6)
eye	3.0 (2.8– 3.4)	2.9 (2.5– 3.4)	3.0 (2.8– 3.2)
naris to eye	2.4 (2.0– 2.8)	2.3 (1.8– 2.6)	2.3 (2.1– 2.7)
femur	10.2 (9.7–11.4)	9.9 (8.6–10.8)	9.1 (8.3– 9.8)
tibia	11.9 (11.1–13.0)	11.1 (9.7–12.5)	10.5 (9.9–11.2)
fourth toe	10.3 (9.0–11.3)	9.4 (7.9–10.6)	8.8 (8.2– 9.7)
tibia/snout-vent ratio	53.5 (50.4–56.5)	48.9 (45.6–51.3)	49.2 (47.2–51.9)

Two samples of small frogs, from the Sierra de Neiba and the Cordillera Central, merit special attention. The series from the Sierra de Neiba consists of nine frogs from three localities ranging in elevation from 4750 feet to 5950 feet; there are eight adult males and one juvenile. The Cordillera series is made up of nine adult male frogs taken while calling; the elevation for part of this lot is 5000 feet (Valle de Culata). The specimens from 4 miles (7 km) north of Constanza have no recorded elevation, but are from above 5000 feet. These two small series are distinctly different from *abbotti* and are quite like *audanti* from the Massif de la Selle. The bold postanal triangle and the conspicuously banded limbs ally these small frogs with *audanti;* all are from high elevations. The voice of the Cordillera specimens resembled the high-pitched calls of *audanti* more than the lower calls of *abbotti*. At Valle de Culata these *audanti* and *abbotti* were heard calling in the same abandoned field, which was grown up in *Pteris* and blackberries. The call of *audanti* at this locality reminded me very distinctly of that of *E. auriculatus* in Cuba — a long series of telegraphic clicks (= "tucks") with an occasional, almost inaudible "wheep" at the end of the series. The *abbotti* call at this locality was that typical for the species throughout its range, and was quite obviously different from the call of *audanti*.

It is remarkable that, despite the large number of frogs which have been collected from the Cordillera Central, *audanti* is presently known only from the Valle de Culata region. This valley is not especially distinctive, being rather small and mostly cut over or burned for pasture.

E. audanti is an upland species, with apparently isolated populations; the Sierra de Neiba and Cordillera populations differ not only from one another but also from the La Selle form. For the Sierra de Neiba population I propose the name:

ELEUTHERODACTYLUS AUDANTI NOTIDODES[1] new subspecies

Holotype. MCZ 43204, an adult male, from 20 km (11.7 miles) southwest Hondo Valle, elevation 5950 ft., Independencia Province, República Dominicana, one of a series taken 11 August 1963 by David C. Leber and Richard Thomas. Original number ASFS V371.

Paratypes. ASFS V372–74, AMNH 71990–92, same data as type; ASFS V385, 14.5 km (8.4 miles) SW Hondo Valle, 4750 ft., San Rafael Province, República Dominicana, 11 August 1963, R. Thomas; MCZ 43205, 25 km (14.5 miles) S Elías Pina, 5000 ft., San Rafael Province, República Dominicana, 17 August 1963, A. Schwartz.

Diagnosis. A subspecies of *E. audanti* characterized (in males; females unknown) by larger size than *a. audanti* (male *a. audanti* to 18.4 mm, male *a. notidodes* to 21.9), longer hind legs, ratio of tibia/snout-vent length higher (46.5 in *notidodes*, 43.8 in *audanti*), little or no dark ventral pigmentation, and hind leg crossbars distinct but not prominently set off from ground color by pale outlining.

Description of type. An adult male with the following measurements (in mm) and ratio: snout-vent length, 21.9; head length, 7.5;

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[1] From the Greek *notis*, *notidis*, moisture, wet, and *-odes*, dweller.

head width, 7.4; diameter of tympanum, 1.2; diameter of eye, 2.7; naris to eye, 2.2; femur, 7.9; tibia, 10.1; fourth toe, 8.6; tibia/snout-vent length, 46.1. Head width equal to head length; snout truncate with nares conspicuous at anterior end of canthus rostralis; diameter of eye greater than distance from naris to anterior corner of eye; interorbital space 2.6, about equal to diameter of eye; diameter of tympanum much less than diameter of eye, distance from tympanum to eye equal to about three-quarters diameter of tympanum. Digital discs present, that of digit three the largest and equal to about two-thirds area of tympanum. Fingers moderate in length, unwebbed, 3–4–2–1 in order of decreasing length; subarticular tubercles well developed, pale gray. Toes moderate in length, unwebbed, 4–3–5–2–1 in order of decreasing length; subarticular tubercles dark gray and prominent. Heels touch when femora are held at right angles to body axis. Dorsum finely warty or shagreened with a raised median line from snout to above vent. Throat and belly granular; vocal sac present, large, extending posteriorly to between forelimbs, heavily glandular anteriorly. Inguinal glands absent. Posterior surface of thighs with large juxtaposed rounded granules. Tongue small, oval, entire, free behind, its greatest width about one-half that of floor of mouth. Vomerine teeth in two sharply oblique patches, beginning within the median border of the choanae, and separated from the choanae by a distance equal to slightly less than the diameter of a choana, and from each other by a distance equal to the length of one tooth row.

Coloration of type in life. Dorsal ground color tan with a darker brown interocular bar and a scapular X; snout, anterior to interocular bar, slightly paler than back; area between interocular bar and two anterior arms of X suffused with darker brown; back in general rather uniformly tan, but on the sides this breaks down into a series of about four lateral bars, separated from one another by creamy gray from the belly. Hindlimbs tan with two crossbars on the thigh, neither especially prominent and neither outlined with pale color; a more conspicuous crural cross-bar, vaguely outlined with pale color; and a single cross-bar on the pes. Forelimbs with one antebrachial bar and a wrist bar. A prominent dark bar from the snout through the eye to the forelimb insertion and covering the upper half of the tympanum. A prominent and very dark brown postanal triangle, extending onto the underside of the thighs. Ventral ground color creamy gray with scattered dark brown stippling, most concentrated on the vocal sac and undersides of the limbs. Iris silvery above.

Variation. Variation in measurements and ratios is shown in Table III. Structurally all the paratypes resemble the type. The rather widely separated vomerine teeth and the angulated arrangement of the two series in relationship to one another are common features.

TABLE III. Means and extremes of three populations of *Eleutherodactylus audanti.* (Females unknown from Sierra de Neiba and Cordillera Central. Sample from Haiti consists of the ten largest specimens of each sex.)

	E. a. audanti [Haitian uplands]	*E. a. notidodes* [Sierra de Neiba]	*E. a. melatrigonum* [Cordillera Central]
	10♂	8♂	9♂
snout-vent length	17.4 (16.2–18.4)	19.9 (17.9–21.9)	18.2 (17.6–20.3)
head length	6.1 (5.7– 6.4)	7.0 (6.5– 7.5)	6.5 (6.0– 6.9)
head width	6.3 (5.8– 6.6)	7.3 (6.3– 7.9)	6.6 (6.1– 7.3)
tympanum	1.1 (0.9– 1.3)	1.2 (1.0– 1.4)	1.2 (0.9– 1.4)
eye	2.4 (2.2– 2.5)	2.8 (2.4– 3.1)	2.6 (2.0– 3.0)
naris to eye	1.7 (1.5– 1.8)	2.2 (2.0– 2.4)	1.9 (1.6– 2.2)
femur	6.6 (6.1– 7.0)	7.7 (6.9– 8.5)	7.2 (6.4– 8.0)
tibia	7.6 (7.2– 8.0)	9.9 (8.4–10.1)	8.2 (7.8– 8.5)
fourth toe	6.6 (5.9– 7.1)	8.0 (7.2– 8.6)	7.0 (6.6– 7.5)
tibia/snout-vent ratio	43.8 (40.8–46.8)	46.5 (44.7–48.3)	45.0 (40.9–47.4)
	10♀		
snout-vent length	23.1 (22.1–25.3)		
head length	8.1 (7.4– 8.6)		
head width	8.5 (7.3– 9.2)		
tympanum	1.5 (1.2– 1.6)		
eye	3.0 (2.7– 3.2)		
naris to eye	2.2 (2.0– 2.4)		
femur	9.1 (8.0– 9.8)		
tibia	10.1 (9.0–10.8)		
fourth toe	9.2 (8.4– 9.8)		
tibia/snout-vent ratio	43.6 (38.6–47.1)		

In coloration, the paratypes are quite variable. All but one were tan in life, but only a single specimen has the rather uniform dorsal pigmentation of the type. In all, the leg bars are more prominent than in the type, although never outlined boldly with paler color. Five specimens have a dark tan dorsum, somewhat irregularly pigmented, with a vague pair of pale reversed parentheses, dark interocular bar, scapular X, and pale snouts. Only one of these normally colored specimens has any indication of ventral mottling, and this is sparse and confined to the sides of the abdomen. All the other individuals have only faint dark stippling ventrally. Two males have a pinkish orange dorsum with irregular dark brown mottling on the limbs, sides, sacrum, and head — the typical asymmetrical *audanti* pattern described in detail by Cochran. Their dorsal blotching carries over onto the venter, but is not heavy there. The smallest paratype (snout-vent 11.1 mm) is pale pink, with prominent limb bars, but with no irregular dark mottling.

Comparisons. E. a. notidodes requires comparison both with the nominate race and with *E. abbotti,* which occurs with it. Compared with *a. audanti, notidodes* reaches a larger size, and averages greater in all measurements. There is virtually no overlap of extremes in measurements of head length, eye, naris to eye, femur, tibia, and fourth toe. *E. a. notidodes* has a longer tibia than does *a. audanti,* although the overlap of the ratios is great. Both subspecies are much alike in coloration and pattern; both show some individuals with asymmetrically blotched dorsal pigmentation. Both have a dark postanal triangle and both show dark limb bars, although those of *notidodes* are not outlined in paler color. The ventral pigmentation is much heavier in *a. audanti*; the *notidodes* with the heaviest ventral pigmentation is lighter than the most lightly pigmented *audanti.*

Compared with male *abbotti* from the interior highlands, male *notidodes* reach a larger size (21.9 vs. 18.9) and are longer snouted (naris to eye 2.2 [2.0–2.4] in *notidodes,* 1.9 [1.7–2.0] in *abbotti*). All other measurements show a great deal of overlap, although *notidodes* averages higher in every measurement except tympanum diameter (1.2 in both species) and femur (7.7 in both species). The tibia/snout-vent length ratio averages greater (47.9) in *abbotti* than in *notidodes* (46.5). None of these measurements is so helpful as pattern for differentiating the two species; by means of the brown postanal triangle and the heavily banded legs, they can be distinguished without difficulty.

The vomerine teeth may prove to be useful in differentiating the two subspecies of *E. audanti.* The teeth in *a. audanti,* although patch-like, seem to be arranged more horizontally than the series in *notidodes*; in the latter subspecies the patches appear to be more diagonal, the two series directed toward one another posteriorly in a broad V.

The small series of *E. audanti* from the Constanza region in the Cordillera Central may be known as:

ELEUTHERODACTYLUS AUDANTI MELATRIGONUM[1] new subspecies

Holotype. MCZ 43206, from 7 km (4 miles) north of Constanza, La Vega Province, República Dominicana, one of a series taken 7 July 1963, by David C. Leber and Richard Thomas. Original number ASFS X8774.

Paratypes. ASFS X8773, X8775–77, same data as type; AMNH 71993–96, 5.1 miles north of Constanza, Valle de Culata, 5000 ft., La Vega Prov., República Dominicana, 8 July 1963, D. C. Leber, R. Thomas.

Diagnosis. A subspecies of *E. audanti* characterized (in males; females unknown) by moderate size (male *a. audanti* to 18.4, *notidodes* to 21.9, *melatrigonum* to 20.3 mm), intermediate length of tibia, hindleg crossbars distinct and variously outlined in paler color, although never so boldly as in *a. audanti*, and pinkish belly with scattered dark chromatophores.

Description of type. An adult male with the following measurements and ratio: snout-vent length, 20.3; head length, 6.9; head width, 7.3; diameter of tympanum, 1.4; diameter of eye, 3.0; naris to eye, 2.0; femur, 7.6; tibia, 8.3; fourth toe, 7.3; ratio of tibia/snout-vent length, 40.9. Head width greater than head length; snout truncate with nares conspicuous at anterior end of canthus rostralis; diameter of eye greater than distance from naris to anterior corner of eye; interorbital space 2.8, slightly less than diameter of eye; diameter of tympanum much less than diameter of eye, distance from tympanum to eye equal to about three-quarters diameter of tympanum. Digital discs present, that of digit three the largest and equal to about three-quarters area of tympanum. Fingers moderate in length, unwebbed, 3–4–2–1 in order of decreasing length; subarticular tubercles well developed, dark gray. Toes moderate in length, unwebbed, 4–3–5–2–1 in order of decreasing length, subarticular tubercles dark gray and prominent. Heels touch when femora are held at right angles to body axis. Dorsum very finely warty, warts most prominent on upper eyelids and upper surface of hindlimbs; a faint, fine, raised line from snout to above vent. Throat and belly granular; vocal sac present, large, extending posteriorly to between forelimbs, heavily glandular. Inguinal glands absent. Posterior surfaces of thighs with large, rounded, juxtaposed granules. Tongue small, oval, entire, free behind, its greatest width about one-half that of floor of mouth. Vomerine teeth in two oblique patches, beginning

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[1] From the Greek *melas*, black, and *trigonon*, triangle.

well within the median border of the choanae, and separated from the choanae by a distance equal to twice the diameter of a choana, and from each other by a distance equal to slightly more than the length of one tooth row.

Coloration of type in life. Dorsal ground color medium tan with a black interocular bar, a black scapular X, its two anterior arms forming with the interocular bar a slightly darker occipital triangle; a dark gray pair of dorsolateral lines and two rather diffuse sacral spots; the two dorsolateral lines broken up posteriorly to form a series of three or four dark dorsolateral spots which approach the vent, forming a dark gray V above it; sides tan, heavily dotted with dark gray. Hindlimbs tan with two faint crossbars on the thigh, neither especially prominent and neither outlined with pale color; a more conspicuous crural crossbar, vaguely outlined with pale color; and a single dark crossbar indicated on the pes. Forelimbs with one antebrachial and one wrist bar. A prominent dark brown bar from the snout through the eye to the forelimb insertion and covering the upper half of the tympanum. Ventral ground color pinkish with some dark gray stippling, especially on the yellow vocal sac and undersides of limbs. Iris silvery above.

Variation. Variations in measurements and ratios are shown in Table III (p. 382). The vomerine series are widely separated and vary in angulation from almost straight to oblique, with the latter the more common condition.

Three of the paratypes have median dorsal pale hairlines which were creamy in life; all have some sort of dorsolateral dark markings, even if the dorsal ground color is dark brown, which separate the dorsal color from the lateral dotting or spotting. The interocular bar, scapular X and sacral spots are common features, although the latter is often almost completely obscured by the dark dorsal pigmentation. The black to dark brown postanal triangle is always conspicuous, and the leg and arm bars are likewise bold, and at times even outlined with pale color. The ventral ground color was pinkish in life, with rather uniform dark brown stippling which never formed ventral blotches or mottling. No specimen shows any indication of the pale dorsum and asymmetrical dark patches of the other two subspecies, although presumably this condition occurs.

Comparisons. E. a. melatrigonum is intermediate between *a. audanti* and *a. notidodes* in all measurements except that of tympanum diameter. The ratio of tibia/snout-vent length is likewise intermediate. The localities whence *a. melatrigonum* is known are, of course, not intermediate between those of *a. audanti* and *a. notidodes.* In both dorsal and ventral pigmentation and pattern, *a. melatrigonum* resembles *a. notidodes* more closely than *a. audanti.* The hindlimb bars of *a. melatrigonum* are slightly more prominent than those of *a. notidodes,* and slightly less prominent than those of *a. audanti.* No *a. melatrigonum* has the venter blotched, as is usually the case in *a. audanti.* As noted above, there are no specimens of *a. melatrigonum* available at present showing the pale dorsum with asymmetrical blotching which occurs in both *a. audanti* and *a. notidodes.*

From *E. abbotti,* with which *E. a. melatrigonum* occurs, the latter can be best distinguished by its prominent postanal triangle and more conspicuously banded limbs. Male *melatrigonum* reach a larger size than do male *abbotti.* All measurements overlap, at times rather widely; the measurement with least overlap is that of the tibia (8.5–9.3 in upland *abbotti,* 7.8–8.5 in *a. melatrigonum*). The ratio of tibia/snout-vent length averages less in *a. melatrigonum* (45.0) than in *abbotti* (47.9), although the extremes overlap. Lower ratios are consistently those of *a. melatrigonum* (40.9–47.4), while higher ratios are those of upland *abbotti* (45.5–51.1).

Remarks. The discovery of two subspecies of *E. audanti* outside the La Selle-La Hotte massif in southern Haiti indicates that this species probably occurs throughout the higher mountains of much of the República Dominicana. The Sierra de Neiba appears to be a favored haven for high-mountain south island species which have been able to cross the Cul-de-Sac–Valle de Neiba plain, or to cross the intervening strait when the plain was flooded. In addition to *E. audanti, E. parabates* (which is a north island representative of the south island *E. ventrilineatus-E. jugans* group) is another species of frog which has distinctly south island affinities, and occurs only in the Sierra de Neiba. *E. audanti,* on the other hand, has been able to extend its range farther north into the Cordillera Central, and in so doing has been able to cross the rather xeric but high Valle de San Juan. It is likely that *E. audanti* occurs in the central Haitian mountains as well, since these are continuous with the Dominican Sierra de Neiba and Cordillera Central; the Haitian mountains are very poorly known herpetologically. It is, of course, possible that *audanti* is a north island species, having evolved in the uplands of the Cordillera, and thence expanded southward into the Sierra de Neiba, across the Cul-de-Sac into the Massif de la Selle and thence into the Massif de la Hotte. Neither explanation is better substantiated than the other.

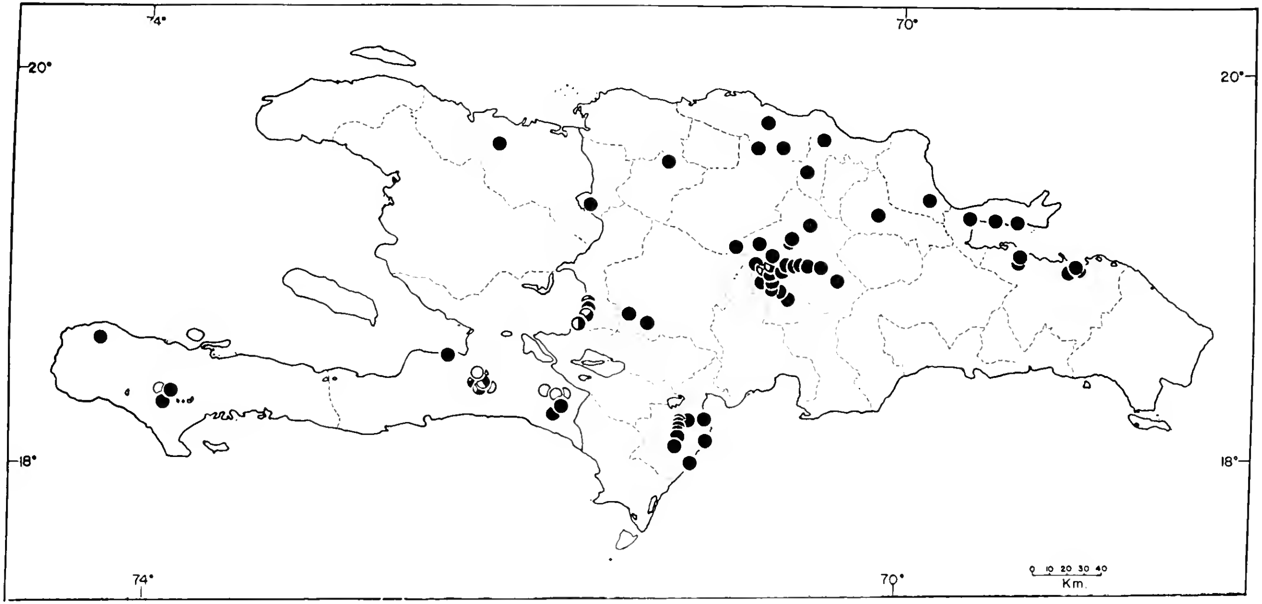

Fig. 2. Hispaniola, showing the known distribution of *E. abbotti* (solid circles) and *E. audanti* (open circles); semi-solid circles represent localities whence both species have been taken. Semi-solid circles in the Sierra de Neiba represent localities for *E. abbotti* and *E. audanti notidodes*; semi-solid circles in the Cordillera Central represent localities for *E. abbotti* and *E. audanti melatrigonum*.

ELEUTHERODACTYLUS MINUTUS AND *ELEUTHERODACTYLUS HAITIANUS*

These two species present an even knottier problem than do *E. abbotti* and *E. audanti.* Regarded by Cochran as two distinct species, *minutus* and *haitianus* are both known only from the Cordillera Central in the República Dominicana. Both seem to be small forms, with *haitianus* the smaller (but see further comments below). Shreve and Williams (1963: 322) regarded *haitianus* as a synonym of the prior *minutus*, and the latter as possibly an upland subspecies of *abbotti.* Cochran (1941: 26) considered that *minutus* had a smooth belly (and was in fact following Noble, 1923: 4, in his original diagnosis of *minutus*) and *haitianus* (= *intermedius*, *sensu* Cochran) had a granular belly. Her figures (pp. 47, 70) show that *minutus* is a rather long-legged species, reaching a known snout-vent length of 18 mm, and that *haitianus* is distinctly short-legged, reaching a known snout-vent length (in the type) of 21 mm. Cochran also commented in the text (1941: 48) that the "paratype" of *minutus* which she examined had a slightly granular belly. Shreve and Williams (1963: 323) later noted that the venter of *minutus* is coarsely granular, in contrast to the more finely granular venters of *abbotti* and *audanti.*

Perhaps the best way to unravel this complicated situation is to discuss the field situation, based on my recent collections only, and then turn to the nomenclatorial problems. In the Cordillera Central, primarily to the north of Constanza and between that town and El Río, there occurs a small frog with a maximum snout-vent length of 17.0 mm in males and 19.4 mm in females. This *Eleutherodactylus* is thus smaller in both sexes than *abbotti,* and males are smaller than male *audanti melatrigonum* from the same general area. The species occurs from 3600 to 6100 feet, in upland broadleaf forests; males call from herbaceous plants, often terrestrial bromeliads, not more than one foot above the ground surface. The call is a single, rising, high-pitched "wheep," almost a pulse, very faint and insect-like. The dorsal ground color varies from tan to brown, with darker sides, and occasionally there are reddish dorsolateral lines separating the dorsal and lateral colors. The dark postanal triangle is fairly distinct, the legs are banded, but rather inconspicuously so at times, and there are remnants of a scapular X. All dorsal pattern elements have a distinctly "muddy" appearance, with no feature being especially clear-cut or prominent (Fig. 3, left). Ventrally, the ground color varies from very pale yellow or cream to gray, and the belly may be either immaculate or have some dark gray dots scattered over it. In addition to the scapular X, there may be a sacral chevron or smudge; the forelimbs are usually somewhat reddish orange.

To the southeast of Constanza, centering in the high Valle Nuevo region, there occurs a small frog with a maximum snout-vent length of 14.8 mm in males and 16.6 mm in females. This species occurs from 5600 to 8000 feet, mainly in pine woods, where it has been found under rocks and logs, and under sheets of moss along a road cut. One calling male was taken about ten inches above the ground on a herbaceous leaf near a small pool in the woods. The call is a descending scale of staccato "beeps." The dorsal ground color varies from tan to very dark brown, almost black in many cases; the brachium is pale reddish, and the ankle often has a reddish brown hue. The dorsal pattern consists of a band usually outlined in dark brown to black, occasionally with a median pale hairline. A common variant is the "dead leaf" pattern — a series of obliterative pale and dark dorsal areas which render the frog inconspicuous against a varicolored brown background. The snout is usually pale and sharply set off from the balance of the back. A series of four dark lateral bars, radiating from the sacrum, is commonplace (Fig. 3, right). The ventral ground color varies from pale yellow (especially on the vocal sac

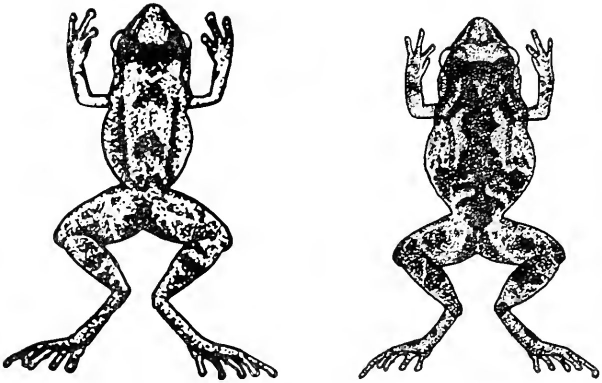

FIG. 3. *Left: Eleutherodactylus minutus*, adult female, ASFS X8938, 16 km N Constanza, 6000′, La Vega Province, República Dominicana; snout-vent length 19.4 mm.
Right: Eleutherodactylus haitianus, adult male, ASFS X8392, 9 km NNE Valle Nuevo, La Vega Province, República Dominicana; snout-vent length 13.9 mm.

in males) to clear white (not gray), and the belly and throat are very heavily spotted with rather large dark brown to black spots in almost all specimens. All dorsal pattern elements are sharp and distinct, including the hindlimb bands which are usually outlined with tan and stand out boldly from the ground color. There is a dark postanal triangle which may be distinct or inconspicuous, depending upon the intensity of the dorsal ground color.

The two forms are almost completely separable on the tibia/snout-vent length ratio. The larger form from north of Constanza averages 46.0 (44.5–49.7) in males and 47.3 (43.9–53.1) in females, whereas the smaller, more southern form averages 41.3 (37.2–45.0) in males and 40.4 (36.1–43.3) in females.

When all aspects of these frogs are considered — the coloration and pattern, morphology, habitat, altitudinal distribution, and vocalization — there seems little doubt that we are dealing with two distinct species.

The nomenclatorial problems involved in allocating names to them are somewhat more complex. I have examined the type of *E. minutus*, but not that of *haitianus*; the latter is, however, well illustrated by Cochran and some pertinent measurements are given. I have had access to the large series of paratypes of *haitianus* and these, although helpful, are so confusing in many ways that they require special discussion.

The type locality of *E. minutus* is "near Paso Bajito, Jarabacoa-Constanza Trail"; Paso Bajito is to the north of Constanza. The elevation is not excessively high; we estimate it at about 4000 feet.

The type of *minutus* (AMNH 11404) is a gravid female with a snout-vent length of 17.3 mm and a tibia length of 8.0 mm. The frog is presently much faded, but dorsally there is a pale zone with a faint scapular X and a faint sacral chevron, distinctly darker sides, only the vaguest indications of leg bars and an interocular bar, and a pale belly with very slightly darker spotting. Of the two species discussed above, the type of *minutus* agrees best with the larger form, which occurs to the north of Constanza, in pattern and size. Additionally, the tibia/snout-vent length ratio in the type (46.2) falls within the extremes of this ratio in the larger of the two species (females, 43.9–53.1), and not within this ratio in the smaller (females, 36.1–43.3). One other factor needs consideration: Noble (1923: 4) described the belly of *minutus* as smooth. Examination of the type of *minutus* shows that the belly is, in fact, rather faintly granular; in this, again, it agrees with the larger of the two species discussed above. (Both the species under discussion have granular bellies; that of the smaller species is more coarsely and heavily granular than that of the larger.) In consideration of the above data, I have no hesitancy in assigning the larger species of frog, described in detail above, to *minutus*.

There remains the possibility, suggested by Shreve and Williams, that *minutus* is an upland race of *abbotti*. Against this suggestion is the fact that the two, although similar in pattern, are quite different in intensity of dorsal pigmentation and in size (largest upland *abbotti* male 18.9, female 25.4; largest *minutus* male 17.0, female 19.4). Vocally they are distinct. Finally, they occur together at two of our recent localities (9.1 miles north of Constanza; 3.3 miles east of El Río), and very close together at another (9.3 miles north of Constanza), where *abbotti* was taken at 6000 feet, *minutus* at 5600 feet. There is no evidence of intermediate specimens, although admittedly intergrades might be extremely difficult to differentiate from the parent populations. Certainly, however, when *minutus* and *abbotti* are collected at the same locality, there is no difficulty in distinguishing one from the other. The tibia/snout-vent length ratio of the two overlaps in both sexes. The means are, however, higher in *abbotti*, averaging 47.9 (45.0–51.1) in males, 48.9 (45.6–51.3) in females; male *minutus* average 46.0 (44.5–49.7), females 47.2 (43.9–53.1).

Turning now to the southern small frogs from the Valle Nuevo region, it would seem quite logical to assume that these specimens are *haitianus*. The type locality, Loma Rucilla, lies about 23.3 miles to the northwest of Valle Nuevo, and the elevation of the type and Loma Rucilla paratypes is expressly stated as 8000 to 10,000 feet. There are three lots of paratypes: USNM 107567, 107569–74, MCZ 23469–74 (17 specimens), Loma Rucilla; USNM 107575–76, Loma Vieja; USNM 107578–85, MCZ 23495–500 (27 specimens), Valle Nuevo. The two paratypes from Loma Vieja are clearly *minutus* in size, pattern, and tibia/snout-vent length ratio, and need not be further considered. Ten of the 35 "*haitianus*" from Valle Nuevo are also *minutus*; if they are actually from Valle Nuevo itself, they represent a new altitude record for *minutus* of 7600 feet. However, the paratypic series is labeled as coming from 6000 to 8000 feet, so that the *minutus* may have come from within the known altitudinal limits of that species.

Twenty-four of the Valle Nuevo paratypes are like the recent Valle Nuevo material discussed above, and are remarkable only in that the series contains females (up to 18.0 snout-vent) and males (up to 15.8) which are larger than the more recently taken specimens. The remaining paratype, a male, has a broad, pale middorsal stripe, a feature not observed in the fresh specimens.

The twenty-four paratopotypes from Loma Rucilla are extremely puzzling. The type specimen was recorded by Cochran (1941: 71) to have a snout-vent length of 21, and thus exceeds all Valle Nuevo specimens in size. Among the paratypes are large females with snout-vent lengths from 18.0 to 19.7, bridging the gap in size between the largest female from Valle Nuevo and the holotype. One of the six males (USNM 107572) is clearly *E. minutus* (thus apparently raising the upper altitudinal limit of that species to at least 8000 feet). Of the five remaining males, four are small and the fifth very large (snout-vent 17.5), in fact larger than any other male.

Loma Rucilla frogs lack the heavily spotted venters of the Valle Nuevo frogs, and have throats which are dark with some paler flecking. The larger frogs have unmarked venters and dark throats, the smaller ones spotted venters; the latter group approximates the recently collected material from Valle Nuevo, although the frogs are larger and have less ventral spotting. Cochran's description of the type, "ventral surfaces . . . clouded with minute darker dots," her drawing of the specimen, and its size agree with the larger Loma Rucilla frogs in detail.

The nomenclatorial problem resolves itself into how many forms (species or subspecies, if any) are involved. It seems rather unusual, for example, that there should be such a large difference in size in adult females between Valle Nuevo and Loma Rucilla. None of the female Valle Nuevo specimens is equal in size to the type or to the larger of the female paratypes from Loma Rucilla. The difference in size, correlated with a difference in ventral pigmentation, noted among the Loma Rucilla specimens, strongly suggests that we may be dealing with two species of frogs (the larger species, *E. haitianus*). Aside from the ventral pigmentation and size, I am unable to differentiate these two "forms" from one another. The tibia/snout-vent length ratio of the larger specimens falls neatly within the extremes of this ratio in specimens from Valle Nuevo. The teeth appear identical, and there are no external characteristics which differentiate them when preserved. Interestingly, a single gravid female (MCZ 40813) from Paraje La Ciénaga, Manabao, in La Vega Province, has a snout-vent length of only 14.7, and is clearly much more like the Valle Nuevo frogs than the larger Loma Rucilla frogs. La Ciénaga lies about 7 miles east of the peak of Loma Rucilla. This single small female suggests very strongly that the larger Loma Rucilla specimens actually are specifically distinct from the more southern frogs.

Another possibility is that there are two subspecies of *E. haitianus* involved, one on Loma Rucilla and the other to the south and east, the Loma Rucilla frogs characterized by larger size and much less heavily pigmented venters. Living specimens may be very distinct, since many colors are evanescent in *Eleutherodactylus*. The least likely solution is that the presumed differences in ventral pigmentation and size are happenstance artifacts of collecting; the large number of specimens from both Valle Nuevo and Loma Rucilla makes this very unlikely.

Without further data in life on the Loma Rucilla populations, there seems only one course open, that of regarding all these frogs as *E. haitianus*, while acknowledging rather important differences between the northern and southern populations.

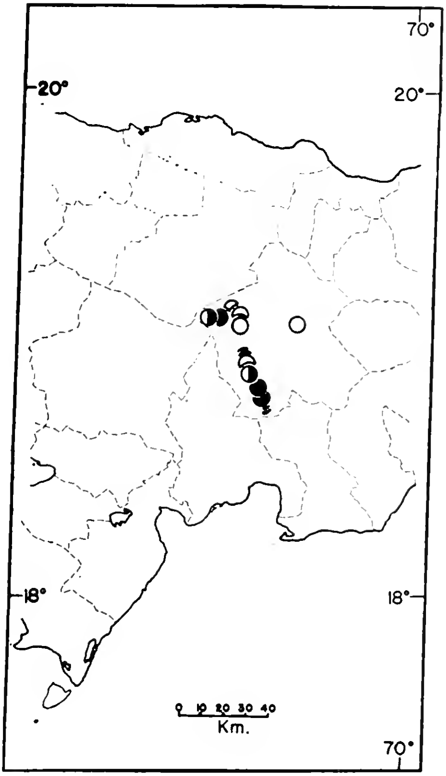

Fig. 4. Central República Dominicana, showing localities for *E. minutus* (open circles) and *E. haitianus* (solid circles). Semi-solid circles represent localities whence both species have been taken.

There is no question that *E. haitianus* is distinct from *E. minutus*. Aside from the habitat and vocal differences discussed above, the two species are easily differentiated on the basis of the tibia/snout-vent ratio; this and other meristic characters are shown in Table IV. That the two species apparently occur together is based entirely on old material with possibly less accurate and carefully taken data than we have for more recently collected specimens; in our experience they do not occur at precisely the same localities. This is also true for the upper altitudinal limits of *minutus*; all the higher elevations are based on old material. Until the older data can be confirmed, it seems appropriate to regard *minutus* as having a lower altitudinal distribution than *haitianus*, although there is an overlap of 500 feet, according to freshly taken and carefully documented material (see Fig. 4 for distribution). There is a need for rather precise notation of elevation in the Cordillera Central. A hike covering several thousand feet elevation may well encompass the altitudinal limits of several species of frogs; the issue may become quickly clouded if all specimens are labeled as coming from between the two extremes in elevation without due regard for more precise altitude.

TABLE IV. Means and extremes of *E. minutus* and *E. haitianus*. For *haitianus* the ten largest of each sex from the Valle Nuevo region were used; for *minutus* all adults of each sex. (Tibia/snout-vent ratio computed for all specimens of each sex from Valle Nuevo, regardless of maturity.)

	E. minutus	*E. haitianus*
	8♂	10♂
snout-vent length	16.4 (15.5–17.0)	13.5 (12.5–14.8)
head length	5.8 (5.5– 6.1)	4.7 (4.4– 5.0)
head width	5.6 (5.3– 6.0)	4.6 (4.2– 5.0)
tympanum	1.0 (0.9– 1.3)	0.9 (0.8– 1.3)
eye	2.2 (2.1– 2.4)	1.9 (1.7– 2.0)
naris to eye	1.4 (1.2– 1.5)	1.1 (1.0– 1.3)
femur	6.6 (6.3– 7.1)	5.1 (4.8– 5.6)
tibia	7.5 (7.3– 7.7)	5.5 (5.0– 5.7)
fourth toe	6.5 (5.8– 6.8)	4.9 (4.5– 5.6)
tibia/snout-vent ratio	46.0 (44.5–49.7)	41.3 (37.2–45.0)
	7♀	10♀
snout-vent length	17.9 (16.0–19.4)	14.8 (12.0–16.6)
head length	6.4 (5.9– 6.9)	5.1 (4.7– 5.8)
head width	6.1 (5.5– 6.6)	5.0 (4.2– 5.6)
tympanum	1.1 (1.0– 1.4)	1.1 (0.7– 1.2)
eye	2.4 (2.1– 2.6)	1.9 (1.7– 2.2)
naris to eye	1.5 (1.3– 1.8)	1.3 (1.1– 1.5)
femur	7.6 (6.9– 8.0)	5.6 (4.7– 6.0)
tibia	8.5 (7.9– 8.8)	5.9 (5.5– 6.5)
fourth toe	7.2 (5.7– 7.7)	5.2 (4.8– 5.7)
tibia/snout-vent ratio	47.3 (43.9–53.1)	40.4 (36.1–43.3)

E. haitianus has not been collected with *E. audanti*. Our collections also indicate that *haitianus* and *abbotti* do not occur together, although the altitudinal ranges of the two overlap by 400 feet. There are specimens of *haitianus* and *abbotti* from Loma Rucilla, the latter from an elevation of 6000 feet. The two species can be separated by the much shorter tibia of *haitianus* and the larger size of *abbotti*. The tibia/snout-vent length ratios of these two species in the Cordillera uplands are: male *haitianus* 41.3 (37.2–45.0), male *abbotti* 47.9 (45.5–51.1), female *haitianus* 40.4 (36.1–43.3), female *abbotti* 48.9 (45.6–51.3).

There are four other small *Eleutherodactylus* specimens from the Cordillera Central which are of interest. These are two males and one female from 11 km (6.4 miles) east of Paso Bajito, 4500 feet (ASFS X8839–41), and a female from Valle Nuevo (MCZ 23498). The two males are in some ways very like *E. abbotti*, except that they are distinctly longer-legged than any male montane *abbotti* (tibia/snout-vent length 55.9 and 54.1). They also appear to be more broad headed. Both have leg bars of the *abbotti* style, and an inconspicuous postanal triangle like *abbotti*. They differ from *abbotti* in ventral pigmentation, since both have a series of dark spots along the lower jaw, and additionally one has some dark ventral dotting. Of the females, one is gravid and has a snout-vent length of 18.1, which is rather small for gravid *abbotti*. These two frogs, from two widely separated localities (MCZ 23498 is a paratype of *haitianus*), are very similar dorsally in that the pattern consists of a pale snout, a very dark chestnut triangle from the interocular bar onto the sacrum where it meets, apex to apex, with another triangle which has its base across the groin. The ground color is a dull orange-tan. There is a prominent postanal triangle, but no other hindlimb markings except dark ankles. Ventrally, these frogs have some faint stippling on the throat and a series of dark spots along the lower jaw margin. Whether these two females are correctly associated with the two males above is unknown. At least the Paso Bajito female has a tibia/snout-vent length ratio of 48.1, a figure which is included within the known range of Cordillera *abbotti*. The Valle Nuevo female, on the other hand, has a ratio of 40.0, which is far below all Cordillera *abbotti* females, and within the extremes of female *haitianus*, a species with which it is definitely not associated.

I have not assigned any of the above four specimens to any species. They may represent one or two new species of small Cordilleran frogs, or they may be aberrantly long-legged or pigmented individuals of well-known upland species.

RELATIONSHIPS OF SMALL HISPANIOLAN FROGS

Of the four species discussed in the present paper, three are clearly members of the *auriculatus* group — i.e., *E. abbotti*, *E. audanti*, and *E. minutus*. As in other members of the group, the presence of a granular venter, enlarged digital discs, short patch-like vomerine series, and an external vocal sac indicate their affinities. *E. haitianus* probably should likewise be considered a member of this assemblage. It differs from the others in having much smaller digital discs and a somewhat more squatty habitus. All four species lack inguinal glands; all four have the peritoneal covering of the testes completely pigmented with jet black chromatophores, while the peritoneal covering of the ovaries has scattered black to gray chromatophores. This dark gonadal pigmentation is a phenomenon which occurs sporadically in Antillean *Eleutherodactylus*, without apparent regard for the affinities of the species. For instance, it occurs in the *dimidiatus* group (*jugans*, *parabates*, *ventrilineatus*), in the *ricordi* group (*zugi*), as well as in the *auriculatus* group.

There is a possibility that *E. haitianus* should be assigned to the *varleyi* group, in which are presently included (Shreve and Williams, 1963: 339): *varleyi*, *glanduliferoides*, and *cubanus*. *E. glanduliferoides* and *varleyi*, in addition to having the *varleyi* group characters of feebly developed discs, short vomerine series, and small size, also have prominent inguinal and popliteal glands; Shreve and Williams commented that *varleyi* did not possess these structures, but they are prominent and orange colored in freshly collected material. I do not know if *cubanus* possesses glands. *E. varleyi* has a pectoral vocal sac; the condition of the vocal sac is unknown in *glanduliferoides*, and *cubanus* apparently lacks a vocal sac. *E. cubanus* and *glanduliferoides* are smooth ventrally; *varleyi* was diagnosed as having a granular belly, although the specimens before me appear to have smooth venters.

E. haitianus resembles the *varleyi* group members in small size, pattern, and short vomerine series. However, the venter is coarsely granular, there are no inguinal or femoral glands, and there is a vocal sac. Black testes are not found in the species *varleyi*, at least. On the basis of all characters, I prefer to regard *haitianus* as a member of the *auriculatus* group, somewhat more divergent than its near relatives in the Cordillera.

Of the four species involved in the present discussion, *abbotti* and *audanti* are more closely related to one another than to *minutus* and *haitianus*. Likewise, *minutus* and *haitianus* are more closely related, with *minutus* more like the *abbotti-audanti* pair.

As noted before, *audanti* is presumably an upland derivative of *abbotti* (which is widespread throughout the island); *audanti* has either evolved in the Massif de la Selle and migrated thence to the La Hotte, on the one hand, and to the Sierra de Neiba-Cordillera Central, on the other, or has evolved in the Cordillera and has moved thence south into the La Selle. More mesic conditions in the lowlands would have facilitated such movement. Both *minutus* and *haitianus*, occurring, as far as is known, only in the Cordillera, may well represent a sequential series *abbotti-minutus-haitianus* (if *audanti* was not developed from *abbotti* in the Cordillera but is an immigrant there), or *abbotti-audanti-minutus-haitianus* (if *audanti* developed in the Cordillera and is an immigrant to the La Selle).

SPECIMENS EXAMINED

Eleutherodactylus abbotti: *Haïti*, *Dépt. du Sud*, ASFS X2797, X2917–22, Camp Perrin; ASFS X3347–51, Carrefour Canon, 500′; MCZ 37729, Marfranc; *Dépt. de l'Ouest*, ASFS X1363–80, X2006–08, X2011, Peneau, 5000′; ASFS X1649, X1795–812, X1818, X1899, MCZ 33546–50, 33552–60, 33562–63, 33565, 33568–73, 33576–79, 33581, 33586–87, 34212, 34221, 34223, 34226, 34229, 34231–32, 34234, 34242–46, 34249, 34250–53, 34256, 34258, 34261–62, 34264, 34272, 34275–76, 34278–81, 34283–84, 34287–89, 34291–92, 34295, 34301–02, 34304–05, + 16 unnumbered specimens, 31729, 31730–32, 31797, Furcy, 5600′; ASFS X3868–69, 2.4 mi. S Kenscoff; MCZ 33280, Morne de Cayette; MCZ 36742, Thiotte; MCZ 31952–53, Savane Zombi, Forêt des Pins; *Dépt. du Nord*, MCZ 3100, 3526, Grande Rivière du Nord. *República Dominicana*, *Barahona Prov.*, ASFS X9642–43, 3.3 mi. NE La Ciénaga; ASFS X9791–94, 0.6 mi. N Las Auyamas, 3000′; ASFS X9809–15, 1.8 mi. N Las Auyamas, 3400′; ASFS X9914–15, 8 km NE Las Auyamas, 2600′; ASFS X9919, V71–83, 10.5 mi. S Cabral, 3500′; ASFS V152, 24 km SW Barahona, 3700′; MCZ 35779–90, del Monte's finca, nr. Barahona; MCZ 35791–96, Herrmann's finca, nr. Paraíso; *Dajabón Prov.*, ASFS V1623–24, 12 km S Loma de Cabrera, 2400′; *Valverde Prov.*, ASFS V1241, 9 km N La Cruz de Guayacanes, 1600′; *Puerto Plata Prov.*, ASFS V1689, 8 km E Imbert, 1100′; MCZ 23545–46, 25 km S Puerto Plata; *Santiago Prov.*, MCZ 23451–55 (8 specimens), Pico Diego de Ocampo; *Espaillat Prov.*, ASFS V1698, 6 km SE Sabaneta de Yásica; ASFS V1955, 2 km N Puesto Grande, 2200′; *María Trinidad Sánchez Prov.*, ASFS V1860, 2 km S El Factor; *Samaná Prov.*, ASFS

V1914, 11 km E Sánchez; MCZ 23530–31, Sánchez; ASFS V1976–82, 5 km W Samaná; *Duarte Prov.*, ASFS V1823–24, 9 km NW Pimentel; *El Seibo Prov.*, ASFS X7835–36, X7975–81, 3.5 mi. S Sabana de la Mar; ASFS X7902–07, 3.3 mi. SW Miches; ASFS X9267, 2.3 mi. SE Miches; ASFS X9337, 1.4 mi. SE Miches; *La Vega Prov.*, ASFS X8564–601, X8880–84, 4 km SW El Río, 4000′; ASFS X8116, 11.5 mi. E El Río, 3800′; ASFS X9162–63, 23 km E El Río, 3050′; ASFS X9197–98, X9225–32, X9240, 6 km E El Río, 3600′; ASFS V1735, 14 km SW La Vega, 1600′; ASFS V1792, 4 km NW La Vega; ASFS V2021, 12 km NE Jarabacoa, 2000′; MCZ 40812, Paraje La Ciénaga, Manabao, Municipio Jarabacoa; MCZ 31129, 40815–18, Constanza; ASFS X8249–54, 1 mi. S Constanza, 4000′; ASFS X8244–48, 7.2 mi. S Constanza, 5000′; ASFS X9085, 11.5 mi. SE Constanza, 5800′; MCZ 23520–21, Loma Vieja, 6000′; ASFS X8754–64, 5.1 mi. N Constanza, Valle de Culata, 5000′; MCZ 40811, La Ciénaga, Culata; MCZ 30588, Aserradero Bermúdez, Constanza; ASFS X9796, 9.1 mi. N Constanza, 6000′; ASFS X8949, 16 km N Constanza, 6000′; ASFS X8826, X8829–30, 6 km W. Constanza, 4250′; ASFS X8892, X8897, Tireo Abajo; MCZ 40806, 43458–65, La Palma, Constanza; MCZ 23481–82, Loma Rucilla; ASFS X8126–27, 1.2 mi. SE Monseñor Nouel, 700′; *San Rafael Prov.*, MCZ 31170–71, 40814, Rancho de la Guardia; ASFS V380–84, 14.5 km SW Hondo Valle, 4750′; ASFS V532, V536, 25 km S Elías Piña, 5000′; ASFS V537, 19 km S Elías Piña, 4000′; ASFS V543–46, 15 km S Elías Piña, 3400′; *San Juan Prov.*, ASFS V393, 7 km W Vallejuelo, 2600′.

Eleutherodactylus audanti audanti: *Haiti*, *Dépt. du Sud*, MCZ 21551–53, foothills, Massif de la Hotte; *Dépt. de l'Ouest*, MCZ 34208–11, 34213–20, 34222, 34224–25, 34227–28, 34230, 34233, 34235–41, 34247–48, 34254–55, 34257, 34259–60, 34263, 34265–71, 34273–74, 34277, 34282, 34285–86, 34290, 34296–300, 34303, 34306–07, + 33 unnumbered specimens, 33551, 33561, 33564, 33566–67, 33574–75, 33580, 33582–85, 37728, ASFS X1813–17, X1819–98, X1900–02, Furcy, 5600′; ASFS X1362, X2009–10, X2012–13, Peneau, 5000′; ASFS X1313–21, 2.5 mi. S Kenscoff, 5600′; ASFS X2362–64, X3870–72, 2.4 mi. S Kenscoff; MCZ 24280 (5 specimens), USNM 72595–97, Morne Cabaio, 7000′; MCZ 21576–89 + 39 unnumbered specimens, La Visite, La Selle range; MCZ 19704–08, USNM 95111–13, Mont la Selle; USNM 85009, "Morne la Selle"; ASFS X1922, X3920–27, Forêt des Pins, 5800′; MCZ 31954–63, Marie Claire, Forêt des Pins; MCZ 24586–88, Bois Pin, nr. Marigot.

Eleutherodactylus audanti melatrigonum: *República Dominicana*, *La Vega Prov.*, MCZ 43206, ASFS X8773, X8775–77, 7 km N Constanza; AMNH 71993–96, 5.1 mi. N Constanza, 5000′.

Eleutherodactylus audanti notidodes: República Dominicana, San Rafael Prov., MCZ 43204, ASFS V372–74, AMNH 71990–92, 20 km SW Hondo Valle, 5950′; ASFS V385, 14.5 km SW Hondo Valle, 4750′; MCZ 43205, 25 km S Elías Piña, 5000′.

Eleutherodactylus haitianus: *República Dominicana, La Vega Prov.*, USNM 107567, 107569–71, 107573–74, Loma Rucilla, 4000–10000′; MCZ 23469–74 + 11 untagged specimens, Loma Rucilla; USNM 107578–85, Valle Nuevo, 6000–8000′; MCZ 23499–500 + 14 untagged specimens, 31588–89, Valle Nuevo; MCZ 40813, Paraje La Ciénaga, Manabao, Municipio Jarabacoa; ASFS X8294–99, X8465, 9 km NE Valle Nuevo, 7400′; ASFS X8392–94, 9 km NNE Valle Nuevo; ASFS X8339–40, 3 km NNE Valle Nuevo; ASFS X8461–62, 11 km SE Valle Nuevo, 8000′; ASFS X8994, 5.3 mi. SE Valle Nuevo, 8000′; ASFS X9070–76, 8.4 mi. SE Valle Nuevo, 7900′; ASFS X8676, 8.9 mi. SE Valle Nuevo, 8000′; ASFS X9083, 15 km SE Constanza; ASFS X8929, 16 km SE Constanza, 5600′; ASFS X9153, 11.8 mi. SE Constanza, 5800′.

Eleutherodactylus minutus: *República Dominicana, La Vega Prov.*, USNM 107572, Loma Rucilla, 4000–7000′; AMNH 11404, MCZ 9338, Paso Bajito; ASFS X9241, 12 km E El Río, 3600′; ASFS X8713, X8795, 9.1 mi. N Constanza, 6000′; ASFS X8790, X8938–47, 16 km N Constanza, 6000′; ASFS X9145, 12.6 mi. SE Constanza, 6100′; USNM 107575–76, Loma Vieja, 6000′; MCZ 23495–97 + 6 untagged specimens, Valle Nuevo.

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TWO NEW FISHES OF THE MYCTOPHID GENUS *DIAPHUS* FROM THE ATLANTIC OCEAN

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TWO NEW FISHES OF THE MYCTOPHID GENUS *DIAPHUS* FROM THE ATLANTIC OCEAN

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No. 9 — *Two New Fishes of the Myctophid Genus* Diaphus *from the Atlantic Ocean*

By Basil Nafpaktitis

INTRODUCTION

During the course of a revisionary study of the myctophid genus *Diaphus*, representatives of two undescribed Atlantic species were found. These two, *Diaphus bertelseni* and *Diaphus lewisi*, are described below.

Of the few authors who have seriously studied *Diaphus*, a specialized myctophid offshoot, some thought it necessary to split the complex into various combinations of genera and subgenera (Goode and Bean, 1895; Fraser-Brunner, 1949; Bolin, 1939, 1959a). Others have maintained the vast array of species within the single genus *Diaphus* (Brauer, 1906; Tåning, 1918, 1928, 1932; Parr, 1928, 1929; Kulikova, 1961). I believe that the former approach has been adopted because of inadequate material and the taxonomic complexity of the group. For reasons which will be presented later in this paper, the inclusion of all the species (except two or, possibly, three) within the single genus *Diaphus* is followed here.

The taxonomic study of the "*Diaphus* complex" is not simple, but a reasonable approach can be made. Some of the difficulties involved are: 1) the close similarity among several species of the group; 2) the limited number of reliable diagnostic characters; 3) the relatively high degree of intraspecific variation; 4) the frail nature and generally poor state of preservation of these mesopelagic fishes; 5) the frequent differences between the luminous organs on the anterior part of the head (important diagnostic characters) of mature specimens and juvenile individuals of the same species; and 6) the sexual dimorphism frequently found in the size and occasionally in the number of these head luminous organs. As a result, the number of nominal species is now close to one hundred. We do not now know which of these are valid, but the number of synonyms may prove to be large.

I am indebted to the Smithsonian Institution and to Dr. Robert Gibbs of the U. S. National Museum (USNM) for providing funds and facilities for the study of material deposited in that institution. Dr. E. Bertelsen of the Danish Marine Biological Laboratory (DMBL) and Dr. C. Richard Robins of the University of Miami Marine Laboratory (UMML) generously made available funds and facilities for study at their respective institutions. Dr. Richard

Backus of the Woods Hole Oceanographic Institution (WHOI), Dr. William J. Richards of the Washington Bureau of Commercial Fisheries (WBCF), and Dr. Gerhard Krefft of the Institut für Seefischerei, Hamburg, have kindly provided material in their care. I am grateful to Dr. Rolf L. Bolin of Stanford University and Dr. Giles W. Mead of the Museum of Comparative Zoology (MCZ), Harvard University, for their kindness in reviewing the manuscript and for offering valuable advice and criticism. Partial financial support from National Science Foundation Grant GF 147 is gratefully acknowledged.

Abbreviations of names of luminous organs on the head, and of body photophores (Fig. 1), are as follows: Dn: dorsonasal; Vn: ventronasal; So: suborbital; Ant: antorbital, a small triangular luminous organ present in several species and lying between the Dn and the anterodorsal aspect of the orbit, not shown in Figure 1; Br: branchiostegal; Op: opercular; PO: thoracic (or pectoral); PVO: subpectoral; PLO: suprapectoral; VO: ventral; VLO: supraventral; SAO: supra-anal; AOa: anterior anal; AOp: posterior anal; Pol: posterolateral; Prc: precaudal.

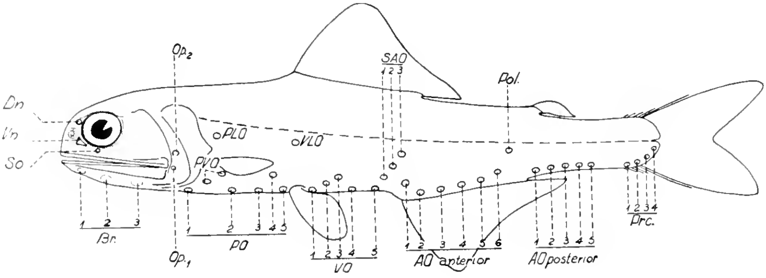

Fig. 1. Diagram of a generalized *Diaphus* showing distribution of the luminous organs of the head and body photophores. Abbreviations after Tåning, 1928, slightly modified.

Measurements were made as follows: standard length (s. l.): shortest distance between tip of snout and end of hypural; head length: from tip of snout to extreme posterior margin of opercular flap; length of upper jaw: from anterior tip of premaxillary to its posterior end; eye diameter: horizontal distance between opposite margins of bony orbit; depth of head: vertical through posterior margin of orbit; depth of body: vertical through base of upper ray of pectoral fin; depth of caudal peduncle: least vertical depth; predorsal: shortest distance between tip of snout and origin of dorsal fin; preventral: shortest distance between tip of snout and base of outermost ray of ventral fin; preanal: shortest distance between tip of snout and origin of anal fin.

All measurements were made with a pair of dividers and recorded in tenths of millimeters. Most measurements were made under a dissecting microscope. Initial values given in the lists of measurements are arithmetic means of all specimens measured; values within parentheses represent extremes. Methods of taking and presenting measurements conform to those used by Bolin (1939).

DIAPHUS BERTELSENI new species

Figures 2–5

Holotype. A 49.0 mm standard length specimen, MCZ 43121, R/V CHAIN, WHOI, cruise 17, station RHB 801, 26 April, 1961, 00°15′S, 18°35′W to 00°15′S, 18°45′W, 10-ft. Isaacs-Kidd Midwater Trawl (IKMT), 0–85–0 m depth.

Paratypes. One, 61.0 mm s.l., MCZ 43122, R/V CHAIN, WHOI, cruise 35, station RHB 971, 22 February, 1963, 02°00′S, 24°57′W to 01°48′S, 24°54′W, 10-ft. IKMT, 0–295–0 m depth.

Two, 21.0–23.0 mm s.l., Dana Collections, R/V DANA station 1223 V, 1 February, 1922, 22°06′N, 84°58′W, ring-trawl, open, conical net, 300 cm in diam. at opening (E300), 600 m wire out.

Additional material examined. One, 9.8 mm s.l., R/V DANA station 1191 I, 14 December, 1921, 17°49′N, 64°54′W, 600 m wire out; one, 11.7 mm s.l., R/V DANA station 1231 II, 6 February, 1922, 24°30′N, 80°00′W, 600 m wire out; one, 8.5 mm s.l., R/V DANA station 1243 III, 16 February, 1922, 21°04′N, 73°48′W, 300 m wire out; four, 9.0–10.5 mm s.l., R/V DANA station 1256 IV, 4 March, 1922, 17°43′N, 64°56′W, 300 m wire out; one, 9.0 mm s.l., R/V DANA station 1257 IV, 6 March, 1922, 17°43′N, 64°56′W, 300 m wire out; one, 9.0 mm s.l., R/V DANA station 1274 III, 27 March, 1922, 17°43′N, 64°56′W, 600 m wire out. All these specimens were captured with stramin-nets, open, conical, 200 cm in diam. at opening (S200).

Description. Body deep and short, its depth 3.5–3.8 in standard length; head large, its length 2.9–3.0 in standard length; diameter of eye 3.4–3.6 in length of head, 2.3–2.5 in length of upper jaw; length of snout equal to or slightly shorter than half the diameter of the eye; upper jaw 1.4–1.5 in length of head and extending less than one diameter of the eye behind posterior margin of orbit; posterior margin of operculum moderately pointed, the point

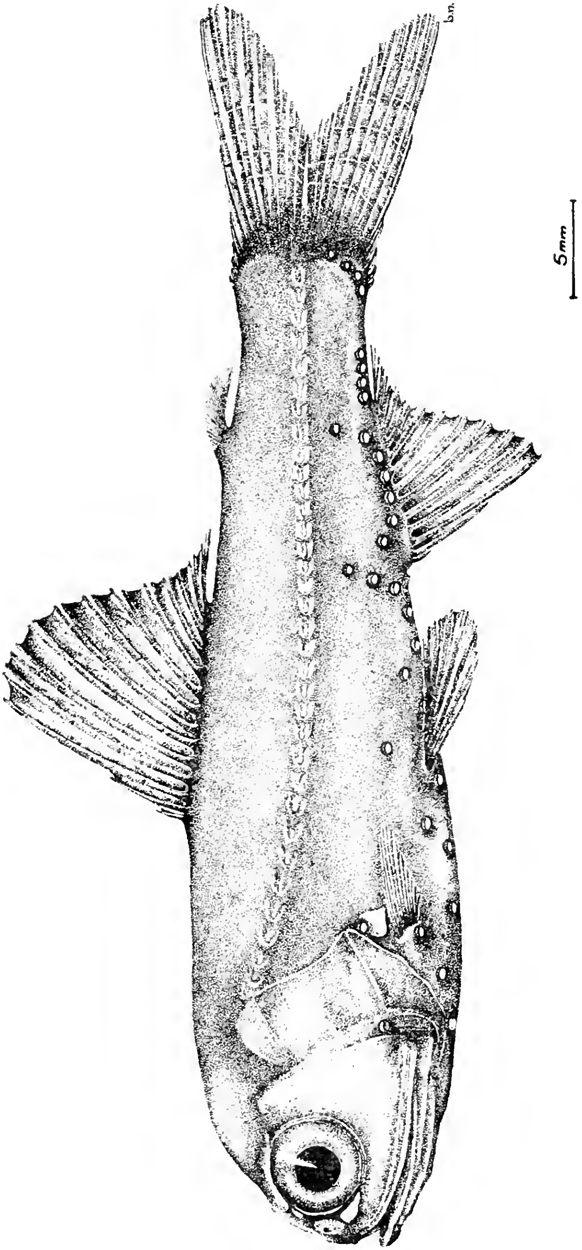

Fig. 2. *Diaphus bertelseni*, holotype, 49.0 mm standard length; R/V CHAIN, WHOI, cruise 17, station RHB 801, depth 85 m, MCZ 43121.

above PLO. Origin of dorsal fin somewhat anterior to base of ventral fin; origin of anal fin behind end of base of dorsal fin; pectoral fin short, its length 1.3 in distance between its base and that of ventral fin; ventral fin just reaching anus; adipose fin somewhat anterior to end of base of anal fin.

Luminous organs. Dn round, in cup-shaped recess, entirely above nostril and well separated from that of opposite side (Fig. 3); Vn considerably larger than Dn, widest at anteroventral aspect of orbit, extending slightly around and under the nostril anteriorly, hardly reaching vertical through anterior margin of lens posteriorly. A conspicuous strip of darkly pigmented tissue present between anterior margin of orbit and luminous organs of head. Body photophores large, close to each other (particularly so in juveniles) and all well below lateral line; distance between PLO and lateral line 3–3½ times the distance between PLO and base of upper ray of pectoral fin; distance between VLO and lateral line 2⅓–2½ times the distance between VLO and base of outermost ventral fin ray; SAO equidistant from each other and on a straight, subvertical line; distance between lateral line and SAO_3 three times the diameter of that organ; AOa_1 elevated, its lowest margin on or slightly above line through upper margins of next two organs of same series; AOa_5 and AOa_6 on a gentle curve with Pol; distance between lateral line and Pol three times the diameter of that organ; AOp_1 above end of base of anal fin; Prc_4 slightly detached from rest

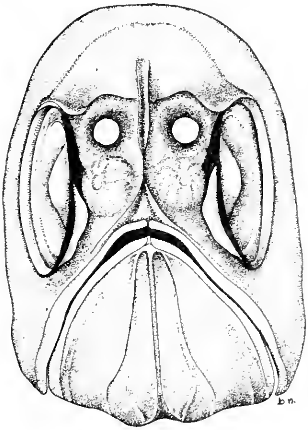

Fig. 3. *Diaphus bertelseni*, front view; semidiagrammatic representation of the luminous organs of the head.

of organs in same series and well below lateral line. Large triangular luminous "scale" associated with PLO (especially well preserved on paratype, MCZ 43122).

Dentition. Both jaws with inner, irregular series of sharp teeth which are conspicuously larger than those in outer series; those on posterior part of premaxillary definitely curved forward (Fig. 4).

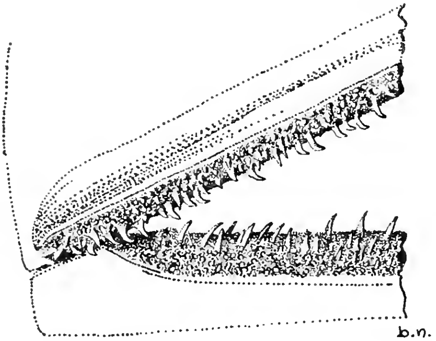

Fig. 4. Lateral view (right side) of posterior parts of jaws, showing dentition in *Diaphus bertelseni* (from holotype).

Counts and measurements. The data which follow are based on the holotype and the three paratypes. Data from non-type material are identified as such. Dorsal fin 14–15; anal fin 15; pectoral fin 11; ventral fin 8; gill rakers on first arch 5+1+12; scales in lateral line 34–35; AO 6 in anterior series and 4 in posterior series. Eight additional specimens, 8.5–11.7 mm s.l., had 6+4 AO, and a ninth had 7+3 on the left and 6+4 on the right side.

Measurements, in per cent of standard length, are as follows: length of head 34.4 (33.3–34.8); diameter of eye 9.9 (9.6–10.2); length of upper jaw 23.8 (23.0–24.4); depth of body 27.0 (26.0–28.5); depth of caudal peduncle 12.7 (12.2–13.0); predorsal 46.6 (44.9–47.8); preanal 69.9 (67.2–71.4); preventral 50.5 (48.4–52.4).

Affinities. In general shape of body and in size and arrangement of photophores, *Diaphus bertelseni* (especially juveniles, Fig. 5) is quite similar to *D. brachycephalus* Tåning. This similarity is superficial, however, and there are many striking differences, such as the lack in *D. bertelseni* of a So, which is so prominent in *D. brachycephalus;* the number and arrangement of the AOa (6, with the first raised in *D. bertelseni,* as opposed to 5 in a straight line); the presence in *D. bertelseni* of a large luminous "scale" at PLO, the same structure being completely absent in Tåning's species, which also possesses strongly curved and broad-based posterior premaxillary teeth.

Differences between *Diaphus bertelseni* and *D. coeruleus* (Klunzinger) are found primarily in the shape, size and position of the Dn; in the head and body dimensions (length of head 2.9–3.0 in standard length, as opposed to 3.5–3.7 in *D. coeruleus;* body depth 3.5–3.8 in standard length, as compared to 4.6–5.0 in *D. coeruleus*); in the length of the upper jaw which, in *D. bertelseni,* extends less than one eye diameter behind the posterior margin of the orbit, while in *D. coeruleus* "Upper jaw . . . hinder end . . . surpasses the eye by more than one eye diameter" (Weber and Beaufort, 1913, p. 169); in the number of AOp (4 in *D. bertelseni,* 5 in *D. coeruleus*).

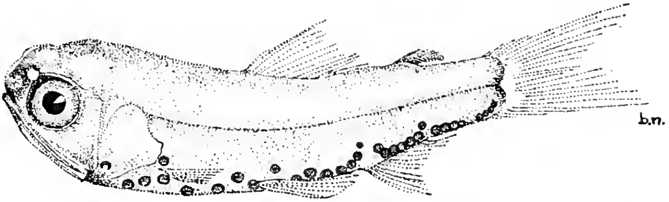

Fig. 5. *Diaphus bertelseni,* juvenile, 9.8 mm standard length; R/V DANA station 1191 I, 17°49′N, 64°54′W, 600 m wire out.

From *Diaphus taaningi* Norman, *D. bertelseni* differs mainly in the size and arrangement of photophores (larger and considerably further below lateral line in *D. bertelseni* than in *D. taaningi*), and in the number of organs in the AO series (6+4, as opposed to 5+5 in *D. taaningi*).

In all cases discussed above, differences in fin ray and lateral line counts are omitted as they are considered by the writer to be of minor diagnostic importance.

Distribution. Pattern and limits of distribution of this species can not now be inferred. The positions of the few stations in which *Diaphus bertelseni* was taken (Fig. 6) suggest that the species is a South Atlantic one. Utilizing the South Equatorial Current, members of this group may enter the North Atlantic while remaining confined to the South Atlantic Central Water Mass. It is also possible that very young individuals are swept away from the northwestern boundaries of the South Atlantic Central Water Mass by the North Equatorial Current and are carried further west and north. The fact that only juveniles were taken in the Antillean and Florida waters, whereas the two south equatorial stations yielded adults, may be purely accidental.

This species is the same as that listed as "*Diaphus* (*sensu* Fraser-Brunner) sp. A" by Backus et al., 1965.

The species is named in honor of Dr. E. Bertelsen, Director of the Danish Marine Biological Institute, Charlottenlund.

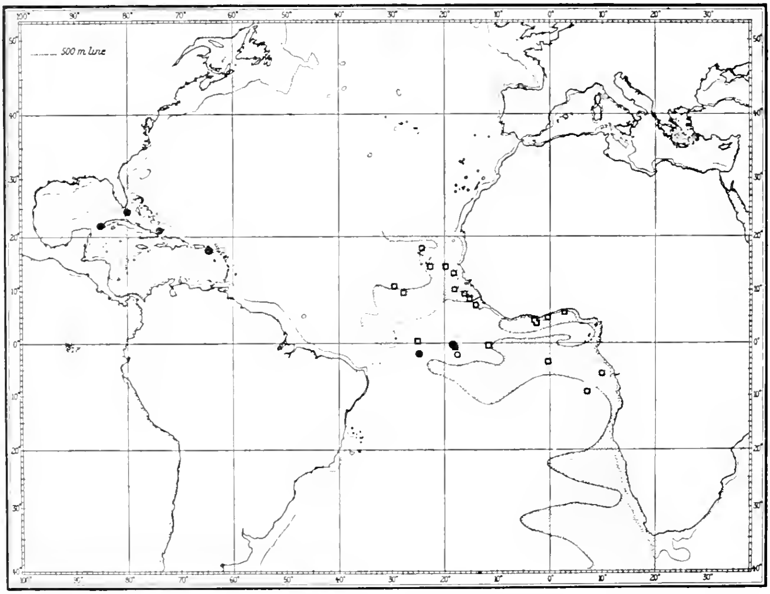

Fig. 6. Chart showing the stations at which *Diaphus bertelseni* (solid dots) and *Diaphus lewisi* (rectangles) were taken. The solid dot at about 17°N, 64°W, represents four DANA stations (1191 I, 14 December, 1921; 1256 IV, 4 March, 1922; 1257 IV, 6 March, 1922; 1274 III, 27 March, 1922). Areas of high productivity are stippled (reproduced to scale from Sverdrup et al., 1942).

DIAPHUS LEWISI new species
Figures 7–11

Holotype. Male, 27.5 mm standard length, Dana Collections, R/V DANA station 4005 XI, 12 March, 1930, 13°31′N, 18°03′W, stramin-net, open, conical, 200 cm in diam. at opening (S200), 50 m wire out.

Paratypes. Two, 20.0–28.5 mm s.l., Dana Collections, data as above for holotype.

Four, 15.6–32.0 mm s.l., MCZ 44000, R/V CHAIN, WHOI, cruise 35, station RHB 972, 23 February, 1963, 00°03′N, 25°00′W to 00°15′N, 25°00′W, 10-ft. IKMT, 0–87–0 m depth.

One hundred, 18.5–31.8 mm s.l., R/V GERONIMO, WBCF, cruise 2, station 138, BCF Cat. No. 370, 19 August, 1963, 09°15′S, 07°06′E, mid-water trawl, depth (?). Eighty specimens in MCZ, MCZ 44001, 20 specimens in USNM, USNM 259155-F1.

Additional material examined. One, 22.0 mm s.l., R/V DANA station 1159 I, 29 October, 1921, 17°55′N, 24°35′W, ring-trawl, open, conical, 300 cm in diam. at opening (E300), 5000 m wire out; 133, 11.0–20.0 mm s.l., R/V DANA station 4003 VI, 9 March, 1930, 08°26′N, 15°11′W, stramin-net, open, conical, 150 cm in diam. at opening (S150), 1000 m wire out; one, 14.5 mm s.l., R/V DANA station 4004 IV, 11 March, 1930, 10°21′N, 17°59′W, stramin-net, open, conical, 200 cm in diam. at opening (S200), 100 m wire out; two, 25.0–26.8 mm s.l., R/V CHAIN, WHOI, cruise 17, station IKT4, 1 April, 1961, 02°10′S, 17°25′W, 10-ft. IKMT, 1800 m wire out; two, 23.0–25.2 mm s.l., R/V CHAIN, WHOI, cruise 17, station IKT5, 3 April, 1961, 00°35′S, 11°30′W, 10-ft. IKMT, depth (?); three, 15.2–15.7 mm s.l., R/V CHAIN, WHOI, cruise 17, station IKT9, 20 April, 1961, 07°15′N, 14°00′W, 10-ft. IKMT, 400 m wire out; one, 20.0 mm s.l., R/V CHAIN, WHOI, cruise 17, station RHB 801, 26 April, 1961, 00°15′S, 18°40′W, 10-ft. IKMT, 0–85–0 m depth; three, 17.5–26.0 mm s.l., R/V CHAIN, WHOI, cruise 17, station RHB 803, 1 May, 1961, 09°27′N, 27°45′W, 10-ft. IKMT, 0–275–0 m depth; 94, 10.2–26.0 mm s.l., R/V CHAIN, WHOI, cruise 17, station RHB 804, 1–2 May, 1961, 10°55′N, 29°30′W, 10-ft. IKMT, 0–42–0 m depth; three, 25.5–28.7 mm s.l., R/V GERONIMO, WBCF, cruise 2, station 166, BCF Cat. No. 181, 25 August, 1963, 05°49′S, 10°00′E, mid-water trawl, depth (?); six, 21.5–29.0 mm s.l., R/V GERONIMO, WBCF, cruise 3, station 130, BCF Cat. No. 971, 26 February, 1964, 04°58′N, 00°30′W, mid-water trawl, depth (?); one, 23.5 mm s.l., R/V GERONIMO, WBCF, BCF Cat. No. 324, 03°28′S, 00°14′W; one, 30.0 mm s.l., R/V PILLSBURY, UMML, station 10, 25 May, 1964, 05°55′N, 02°52′E to 05°58′N, 02°50′E, IKMT, gear depth 0–655–1065–0 m; two, 15.0–18.0 mm s.l., R/V PILLSBURY, UMML, station 36, 29 May, 1964, 03°50′N, 02°37′W, IKMT, gear depth 0–750–0 m; one, 15.2 mm s.l., R/V PILLSBURY, UMML, station 37, 29 May, 1964, 04°00′N, 02°46′W to 04°05′N, 02°50′W, IKMT, gear depth 0–480–490–0 m; five, 23.5–26.8 mm s.l., R/V WALTHER HERWIG, Institut für Seefischerei, station 103, 24 March, 1964, 14°30′N, 22°45′W, IKMT, depth (?); one, 31.0 mm s.l., R/V WALTHER HERWIG, Institut für Seefischerei, station 109, 25 March, 1964, 14°30′N, 19°42′W, IKMT, depth (?); one, 29.2 mm s.l., R/V WALTHER

HERWIG, Institut für Seefischerei, station 129, 4 April, 1964, 09°14′N, 16°00′W, IKMT, depth (?).

Of the additional material examined, those specimens taken by R/V DANA are deposited in the Dana Collections, Charlottenlund, Denmark; the specimens collected by R/V CHAIN and R/V GERONIMO are deposited in the MCZ; those caught by R/V PILLSBURY and R/V WALTHER HERWIG are to be found in the UMML and the Institut für Seefischerei, Hamburg, respectively.

None of the collections examined appears to have been made with closing nets.

Description. Small form; depth of body 3.8–4.3 in standard length; length of head 2.9–3.1 in standard length; diameter of eye 3.4–4.2 in length of head and 2.3–2.9 in length of upper jaw; snout longer than half the diameter of the eye; anterior spine-like end of supraorbital ridge extending forward and downward nearly reaching the posterodorsal aspect of the nostril; upper jaw 1.4–1.5 in length of head and extending one diameter of eye behind posterior margin of orbit; pterotic spine conspicuous; posterior margin of operculum rounded dorsally, moderately pointed posteriorly, the point at or slightly below PLO. Origin of dorsal fin directly above or slightly anterior to base of ventral fin; origin of anal fin behind end of base of dorsal fin; upper rays of pectoral fin reach base of ventral fin; ventral fin nearly reaching origin of anal fin; adipose fin above last 4–5 rays of anal fin.

Luminous organs. Dn apparently fused with Vn, the compound structure beginning at or somewhat higher than the dorsal margin of nostril, extending between latter and anterior margin of orbit and expanding ventrally, its posteroventral tip not reaching vertical through anterior margin of lens; a strip of black tissue separates the preorbital luminous complex from the anterior margin of orbit and extends along the ventral aspect of eye; its posterior end expands into a small pocket-like structure which protrudes into the iris behind the vertical through the middle of lens; inside the pocket-like structure there is a small, round So. The suborbital organ first appears in individuals 16.0–17.0 mm s.l., and in well preserved adult specimens it appears connected with the Dn-Vn complex by means of a very narrow isthmus of luminous tissue. Body photophores of medium size and separated from one another by an interspace at least as wide as the diameter of these organs; PLO and VLO distinctly closer to pectoral and ventral fin bases, respectively, than to lateral line; SAO series of three unequally

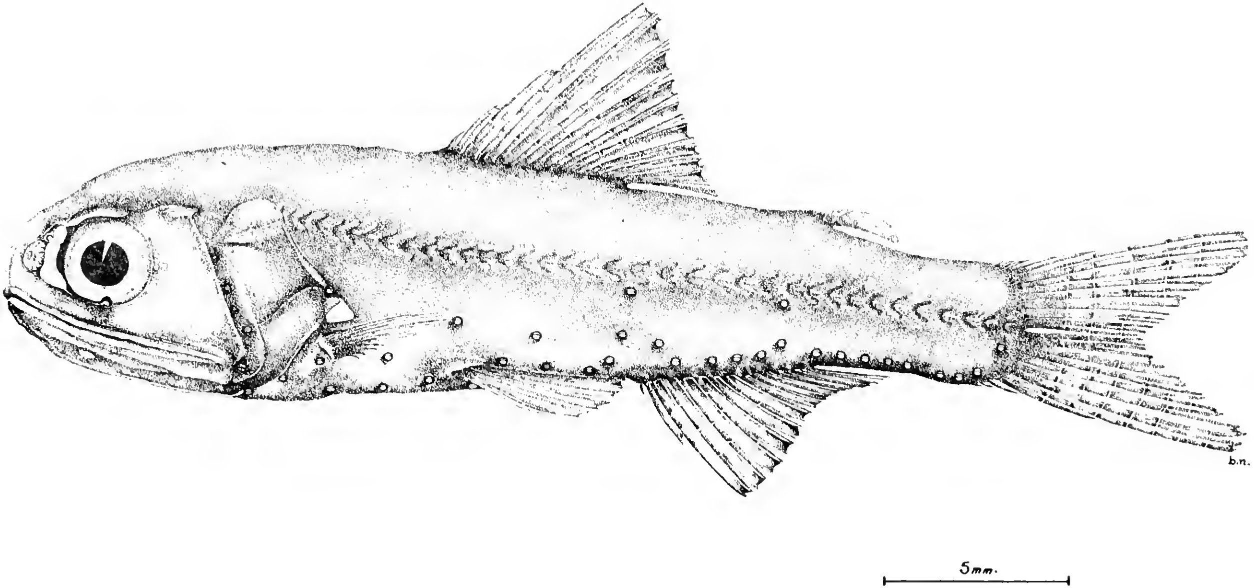

Fig. 7. *Diaphus lewisi*, holotype, male, 27.5 mm standard length; R V DANA station 4005 XI, 50 m wire out. Dana Collections, Charlottenlund, Denmark.

spaced photophores forming a slightly curved and steeply ascending line; distance between SAO_1 and SAO_2 1½–2 times that between SAO_1 and VO_5, distance between SAO_2 and SAO_3 at least 1½ times that between SAO_1 and SAO_2, SAO_3 about its own diameter below lateral line; AOa_1 1–2 times its diameter anterodorsad to AOa_2, last AOa in line with or slightly raised above preceding three or four organs of same series; Pol directly above last AOa and ½–1 times its own diameter below lateral line; AOp_1 above posterior end of anal fin base; Prc_4 distinctly detached from rest of organs of same series and well below lateral line. A triangular luminous "scale" present at PLO.

Dentition. Upper jaw with inner series of strongly recurved, broad-based teeth (Fig. 8); lower jaw with inner irregular series of teeth feebler than those of upper jaw and only slightly curved forward.

Sexual dimorphism. Males are easily distinguished from females by the presence in the former of a conspicuous, roughly triangular antorbital luminous organ (Ant) immediately above and in contact with the Dn-Vn complex (Figs. 7 and 9). This sexual character first appears as a small, diffuse patch of luminous tissue in individuals 18.0–19.0 mm standard length, and attains its maximum size

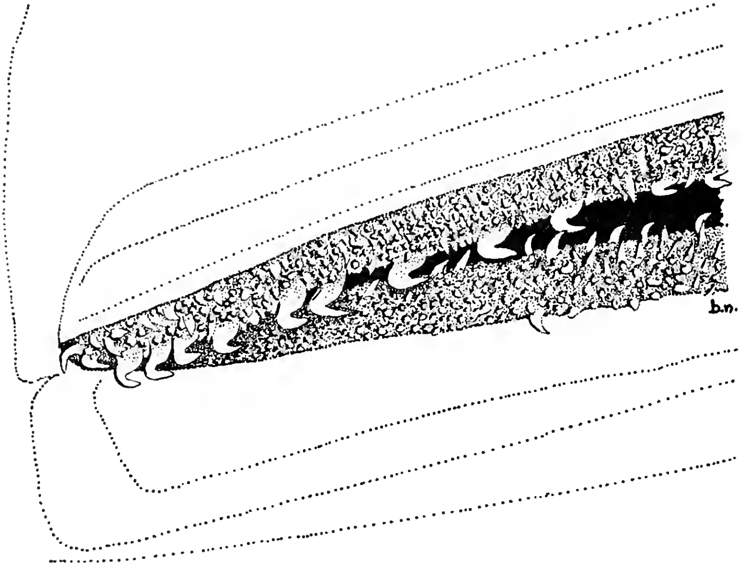

Fig. 8. Lateral view (right side) of posterior parts of jaws, showing dentition in *Diaphus lewisi*.

and its definitive outlines at sexual maturity which, in this small fish, is attained at a size of 27.0–28.0 mm standard length.

Counts and measurements. Meristic data based on 127 specimens are as follows: dorsal fin 13–14 (usually 14); anal fin 14–15 (usually 15); pectoral fin 10–11; ventral fin 8; gill rakers on first arch 7–8 + 1 + 14–15, total 22–24; scales in lateral line 35–36;

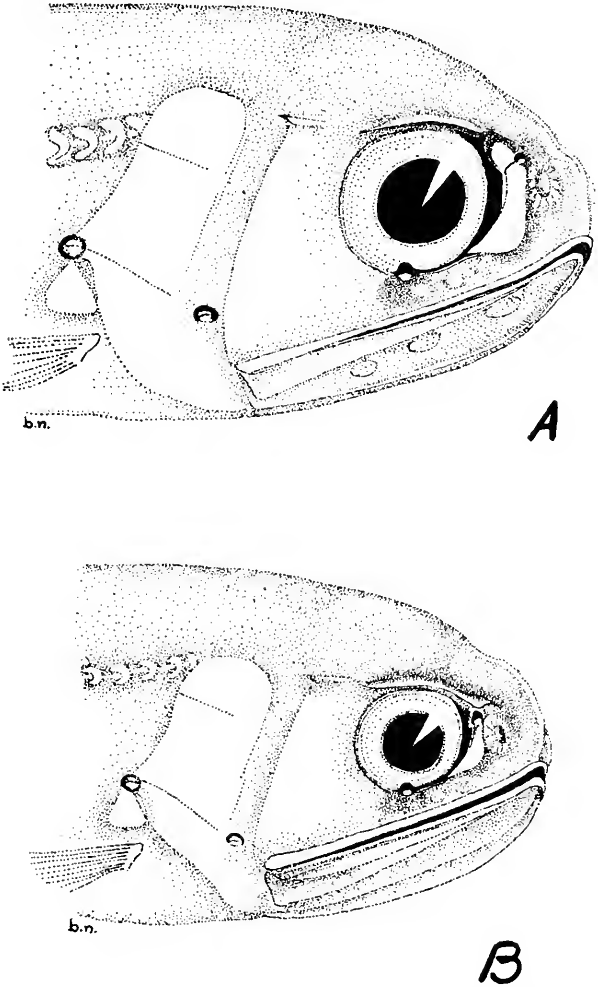

Fig. 9. Sexual dimorphism in the luminous organs of the head in *Diaphus lewisi*. A: male, 32.0 mm standard length; B: female, 27.0 mm standard length.

AOa 5–6 (very rarely 7), AOp 4–5 (very rarely 6). The AO series show considerable variation in number and arrangement not only among individuals but also between two sides of the same individual, the most common patterns being those shown in Figures 7 and 10.

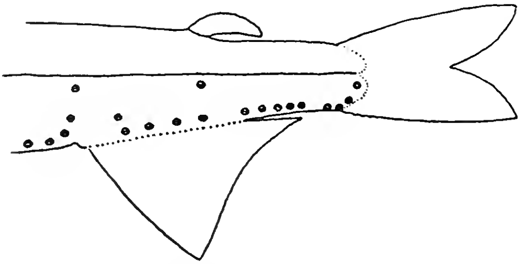

Fig. 10. Caudal region of *Diaphus lewisi*, showing variation in the number and arrangement of the photophores in the AOa series.

Measurements, in per cent of standard length, based on 40 specimens 15.6–32.0 mm s.l., as follows: length of head 33.6 (32.1–35.0); diameter of eye 8.9 (8.1–10.3); length of upper jaw 23.3 (22.0–24.2); depth of body 24.4 (23.0–26.2); depth of caudal peduncle 10.9 (10.0–12.6); predorsal 46.5 (44.8–48.9); preanal 65.4 (62.0–67.0); preventral 47.1 (44.8–48.5).

Fig. 11. *Diaphus lewisi*, juvenile, 11.5 mm standard length; R V CHAIN, WHOI, cruise 17, station RHB 804, 10°55′N, 29°30′W, depth 42 m.

Affinities. *Diaphus lewisi* is a small fish, probably not growing larger than 32–33 mm in standard length. It belongs to the *Diaphus rafinesquei* group which includes *D. rafinesquei* (Cocco) and *D. holti* Tåning in the northeastern North Atlantic, *D. mollis* Tåning, *D. brachycephalus* Tåning, and probably *D. theta* Eigenmann and Eigenmann in the southwestern North Atlantic and, in addition, several other species elsewhere. The main characters common to the members of this group are the three distinct luminous organs on the head (Dn, Vn and So) and the strongly recurved, broad-based premaxillary teeth. *D. lewisi*, although deviating from the typical *rafinesqui* pattern of luminous organs on the head in the fusion of the Dn and Vn, does possess the peculiar premaxillary dentition characteristic of the group.

Diaphus suborbitalis Weber from the Indo-Pacific area has luminous organs on the head which seem to be intermediate between those of the *rafinesquei* group and those found in *D. lewisi*. In Weber's species the Dn and Vn tend to, but have not fused completely. In many other respects *D. suborbitalis* is, according to Weber (1913, p. 91), closely related to *D. fulgens* Brauer, a typical species of the *rafinesquei* group from the Pacific Ocean and one possibly identical with *D. mollis* Tåning. Further discussion of possible relationships among the species mentioned in this paragraph must await a direct comparison of pertinent material.

Distribution. Available data suggest that the area occupied by *Diaphus lewisi* is rather well defined (Fig. 6). Within its range this species is quite common, and the pattern of its distribution is obviously influenced by the hydrography along the west coast of Africa. The cold Benguela Current and the continuous upwelling from depths of 200–300 m account for the remarkably high productivity, the relatively low temperature, and the low salinity of the coastal surface water. These conditions stand in contrast to those of surface waters of the general South Atlantic tropical and sub-tropical areas which are warmer, more saline and low in nutrient content (Raymont, 1963). The belt of fertile water extends approximately 200 km offshore, forming tongues of gradually diminishing plankton density extending outward from the coast (Fig. 6). These tongues correspond to the main water movements that flow away from the coast, as indicated by the outward extension of the isotherms (Sverdrup et al., 1942). The high productivity of the coastal Benguela Current is reflected in the rich zooplankton with which, in turn, may be associated the abundance of marine vertebrate and invertebrate forms (Raymont, 1963).

With a knowledge of the hydrography of the area concerned, the distribution of *Diaphus lewisi* and, no doubt, of other mesopelagic forms becomes meaningful. Relatively abundant along the continental slope of the African west coast and particularly so in areas of high productivity, *D. lewisi* becomes less and less common towards the west. The northernmost limits of its distribution (about 18°N) more or less coincide with the southern limits of the North Atlantic Central Water Mass. A rather marked drop in water temperature at about 18–20°S and in depths of 200–400 m possibly constitutes a barrier to the spreading of the species further south along the west coast of Africa.

The species is named in honor of Dr. Robert E. Lewis, Curator of the Museum of Natural History, American University of Beirut, Lebanon.

DISCUSSION

Taxonomy. The taxonomy of the "*Diaphus* complex," like that of other difficult groups, has been arranged and repeatedly rearranged, especially on the generic level, with little success in achieving a stable system. Inadequate material may have been one of the main reasons for the existence in the literature of so many genera and subgenera. With the increase in the number and size of collections, some students of this group began realizing that they were dealing with the potentially unlimited inventiveness of nature as regards the size, shape and complexity of the luminous organs of the head. They also saw that such morphological features as the "theta" (Greek letter θ) configuration of the body photophores and the number and arrangement of some of the series of these organs (PVO, PO, VO and Prc) seemed, with very few exceptions, highly constant throughout the group. As a result one single genus, *Diaphus,* was accepted and used by them.

Myctophid taxonomy has been heavily dependent on the number and distribution of photophores. It is undoubtedly true that these characters are of great importance in distinguishing the genera within the family. However, at the species level the value of these characters is often questionable. Their inadequacy, in the *Diaphus* group at least, becomes obvious as one grows familiar with: a) the close morphological similarity shown by several species of the group, and b) the relatively high degree of intraspecific variation which often masks interspecific differences.

In contrast to the generally conservative diaphid morphology, the luminous organs of the head show an astonishing variety of sizes, shapes, patterns and numbers. In most cases the role of these organs in interspecific differentiation is decisive.

Of the few diagnostically important characters available to the student of the *Diaphus* group, some have been consistently overlooked. To cite one example: In most studies of *Diaphus* very little, if any, attention has been paid to dentition, a character the importance of which has been repeatedly emphasized by Bolin (1939, p. 124; 1959, p. 20). In his detailed description of the genus *Diaphus,* as exemplified by *Diaphus rafinesquei,* Bolin (1939, p. 124) calls attention to the peculiar dentition of this species and suggests that: "Probably most of the other species now placed in the genus will require re-allocation since examination of several forms has failed to reveal a dentition similar to that found in *Diaphus rafinesquei.*"

Bolin's suggestion subsequently found support in the observation that those forms with sharply recurved premaxillary teeth also had three well-defined luminous organs on the head (Dn, Vn and So). These two features, namely dentition and pattern of luminous organs, seemed important enough to justify generic distinction of the species which possessed them. However, further examination of large numbers of specimens belonging to different diaphid species has revealed that the premaxillary teeth display a series of gradually changing shapes. Between the two extremes, straight and sharply recurved, there exists a series of more or less curved premaxillary teeth. Furthermore, the young of some species (e. g. *Diaphus elucens, D. problematicus,* etc.) have curved teeth, especially on the posterior end of the premaxillary. These teeth are apparently lost and replaced by straight or less-curved ones in older individuals of the same species. Finally, a generic line becomes even more difficult to draw if one considers the existence of forms like *Diaphus lewisi* and, probably, *D. suborbitalis* Weber. The former species (I have not personally examined *D. suborbitalis,* hence I cannot speak with certainty about it), while deviating considerably from the *rafinesquei* pattern of luminous organs on the head, does show the *rafinesquei* kind of dentition.

The gradual change in shape displayed by the premaxillary teeth does not at all diminish the diagnostic usefulness of dentition, especially in the case of juveniles of morphologically very similar diaphid species. Young individuals of *Diaphus fragilis* Tåning and *D. elucens* Brauer, for instance, are very difficult to differentiate. With the numbers and arrangement of their body photophores strikingly similar, luminous organs of the head easily confused (before attainment of their definitive pattern and size), and with horizontal distributions considerably overlapping, the juveniles of these two species can be identified on the basis of premaxillary and particularly dentary teeth shape and size (e. g. lower jaw with inner series of very large, widely but regularly spaced teeth in *Diaphus fragilis,* lower jaw with inner irregular series of denser and much smaller teeth in *D. elucens*).

Turning once again to the character of the luminous organs of the head, we are faced with a situation somewhat analogous to that of the teeth. These organs, in their great variety of designs, can, with some imagination, be arranged in one or more series of progressively increasing complexity. This has certainly been attempted in the past (Parr, 1928, p. 140). However, sound inferences about evolutionary trends of these organs cannot be made on the basis of external morphology alone. A careful histological study of their structure and innervation could probably help us gain some insight into the evolution of the numerous patterns and thus, perhaps, lead us to a better understanding of the phylogenetic relationships among the various species in the group.

Professor Rolf Bolin is of the opinion (personal communication) that there are several divergent lines within the *Diaphus* group. Although I fully agree with his opinion, I feel inclined to disagree with the idea that these divergent lines are, at the present state of our knowledge at least, clear enough to justify a division of the group into more than two genera. An attempt to formalize these lines would lead either to a large number of genera or, at best, to a reasonable number of genera but with several species "suspended" in between. On the basis of the arguments presented above, it is suggested here that all but the species assigned to the genus *Lobianchia* Gatti (e.g. *Aethoprora* Goode and Bean, *Panthophos* Jordan and Hubbs, *Lamprossa* Jordan and Hubbs, *Caelampus* Whitley) be included within the single genus *Diaphus*, without formal division into subgenera (e.g. *Hyperphotops*, *Panthophos* and *Lamprossa*, all three erected by Fraser-Brunner in 1949).

Ecology, speciation and phenotypic similarity. Some speculation on the phenotypic similarity among several myctophid forms is in order here, and should start with a brief consideration of some aspects of oceanic ecology and of possible ways of speciation among high-seas forms. Ecological conditions in the sub-tropical and tropical oceans seem to have been quite stable in geological time (Marshall, 1963, p. 182). Relative differences in physicochemical factors, i. e. temperature, salinity and density, between adjacent water masses and, below the thermocline, between bathymetrically contiguous layers are usually very small. Repeated invasions of these adjacent environments by populations of a given species probably result in some of the more adaptable individuals becoming physiologically adjusted to the small differences. Following this adjustment, which may not require more than slight adaptive changes in the reproductive physiology of the invaders, colonization of the new habitat, or habitats, is under way. Subsequently, one might expect the gene flow between the colonizers and the parent species to decrease. Finally, perhaps through the development of preferential mating and competition ". . . between [the] contiguous populations in the zone of contact and the subsequent elimination of the less well adapted intermediates in this zone. . . ." (Ebeling, 1962, p. 149, from Fryer, 1959), the initial, partial isolation of the populations may be substantially reinforced. Now, if this is the approximate sequence and extent of the major evolutionary events leading to the formation of new species, then it would be reasonable to infer that speciation in many deep-sea fishes does not necessarily involve conspicuous or even readily noticeable structural modifications.

In considering the great morphological similarity among several myctophid forms one should also take into account such evolutionary processes as convergence and parallel adaptations. Hubbs (1941, p. 190) says: "The general tendency of fishes to speciate along parallel courses in correlation with the temperature and salinity of the water is being repeatedly indicated. . . ." Finally, in his discussion of the phenomenon of sibling species, Mayr (1963, p. 57) calls attention to the evidence, found in recent work in developmental genetics, indicating that there is a selective premium on the maintenance of the phenotype. "Any disturbance of the developmental process by a gene mutation will result in a selection pressure in favor of other genes that restore development along the normal, time-tested channels" (Mayr, 1963, from Lerner, 1954, and Waddington, 1956).

The rather strong emphasis placed above on adaptation to apparently minor differences in physico-chemical factors seems to be in conflict with the known ability of adult myctophids to tolerate wide extremes in temperature, salinity and, perhaps, several other ecological factors. In the course of their extensive (several hundred meters) diurnal vertical migrations, these fishes "may well be subjected to much greater differences in temperature than those marking the limits of their distribution" (Fraser-Brunner, 1949, p. 1020). This conflict may be resolved if we assume that during a certain period, or periods, of the year these fishes become, in terms of reproductive physiology, specifically stenothermal and stenohaline. It may also be that survival of the gametes, successful fertilization, or early development fail in the absence of optimal, species-specific physico-chemical conditions. If these assumptions are correct we should expect these optimal ecological conditions to delimit the breeding area and hence the distribution of the species. But, "certainly in the sea we have many suggestions that the distribution of the species is much wider in many instances than the distribution of the breeding population" (Ebeling, 1962, p. 139, from Bullock, 1958). This brings us to another potent environmental factor, namely the oceanic current patterns, and their role in the phenomenon of "expatriation."

Expatriation. Within a breeding area the larvae are restricted to surface or near-surface waters. Just before, or at the very beginning of metamorphosis, these larval forms move to deeper layers. Based on his studies of larval fishes, Tåning (1918, p. 20) writes: "There can . . . hardly be any doubt that the Scopelids [myctophids], when metamorphosis sets in, undergo a thorough change, acquiring a different specific gravity to that which they had as postlarvae, and consequently move down, either actively or passively, to water layers of a specific gravity suitable to their requirements during metamorphosis, and later, after the metamorphosis is completed, ascend once more to the upper layers. In other words, we have here a decided instance of (passive or active) ontogenetic migration." Both as larvae prior to their "ontogenetic migration" and as young right after their ascent to the upper layers, myctophid and other forms with similar life histories are at the mercy of the prevailing current systems in the area concerned. The larvae and young may either be carried away from the breeding area or they may be kept restricted within it (current gyres, eddies, etc.). In the first case the individuals may spread over a wide range, far away from the breeding area of the species to which they belong. Sexual maturity will probably be attained while in environments which, although favorable in terms of satisfaction of purely individual needs, are far from meeting the species-specific reproductive requirements. These individuals are thought to be "expatriated" and reproductively lost to their populations (Ebeling, 1962, p. 139).

Concerning the fate of the "expatriates," Ekman (1953, p. 317) remarks that ". . . it remains questionable whether the species is able to exist independently in the unfavorable region or whether it would not die out there if it were not continuously reinforced from the more favorable regions," and ". . . the unfavorable region is . . . outside the real home of the species, and it [is] . . . possible to contrast the autochthonous main mass of the species which lives in the reproductive area with an allochthonous sterile expatriated contingent in an expatriation area." Bolin (1959b,

p. 142), also, points out that "while straggling adults may exist for long periods in waters far beyond the normal range of the species, permanent populations are restricted to the proximity of the areas where spawning can be successful." During my study of the distribution of the diaphid species in the Atlantic Ocean I have found considerable evidence indicating that many of the diaphid specimens captured off the northeastern coast of the United States are "expatriates" belonging to species the breeding areas of which are well within the tropical and sub-tropical waters.

I am well aware of the weaknesses in my assumptions and arguments. I would like to conclude with a well-worn but nevertheless appropriate statement — a great deal of work remains to be done, especially with regard to the distribution and bionomics of this scientifically and, perhaps, economically important group of mesopelagic fishes.

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THE *AMEIVA* (LACERTILIA, TEIIDAE) OF HISPANIOLA.

II. GEOGRAPHIC VARIATION IN *AMEIVA CHRYSOLAEMA* COPE

By Albert Schwartz and
Ronald F. Klinikowski

CAMBRIDGE, MASS., U.S.A.
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No. 10 — *The* AMEIVA (*Lacertilia, Teiidae*) *of Hispaniola* II. Geographic Variation in Ameiva Chrysolaema Cope

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INTRODUCTION

The largest of the three species of Hispaniolan ground lizards, *Ameiva chrysolaema* Cope, was described in 1868 with the type locality "Gonave Island." Three other names were then applied to this species in rapid succession: *vittipunctata* Cope 1871, *affinis* Fischer 1883, and *regularis* Fischer 1888. Of these, *vittipunctata,* as Cochran (1941: 275-276) has made clear, was apparently described by Cope from a young specimen (snout-vent length 88 mm) which was part of the same series from which he himself had taken the type of *chrysolaema.* Cope, however, gave a different type locality — "city of Santo Domingo" — for *vittipunctata.*[1]

In her revision of the species in "Herpetology of Hispaniola," Cochran (1941: 275–292) considered *vittipunctata* Cope a strict synonym of *A. chrysolaema* Cope. *A. regularis* Fischer was regarded as a strict synonym of *affinis* Fischer, which was accepted as a valid mainland subspecies (a new status since *affinis* had previously been regarded either as a full species or a synonym).

Prior to 1941 two subspecies of *A. chrysolaema* had been described from satellite islands of Hispaniola: *A. c. woodi* Cochran from Ile de la Tortue and *A. c. abbotti* Noble from Isla Beata. These Cochran considered recognizable. A third subspecies, *A. c. boekeri* Mertens (1938: 338), however, from the mainland at Fondo Negro, República Dominicana, was rejected as a synonym of *A. taeniura.*

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[1] Cochran (1941: 245) noted that the type locality of *Celestus* (= ***Diploglossus***) ***weinlandi,*** also described by Cope and said by him to have been collected on Ile de la Gonâve, was incorrect and the specimen actually came from the mainland within 25 miles of Port-au-Prince, Haiti. Since A. C. Younglove who collected the type of *C. weinlandi* in 1868 also collected the type of *A. chrysolaema,* it is appropriate, as Dr. Cochran has done, to restrict the type locality of *A. chrysolaema* to "within 25 miles of Port-au-Prince." If the type of *A. vittipunctata* is actually part of the same series as the type of *A. chrysolaema,* the type locality of the former should likewise be considered the same as that of the latter, despite Cope's statement that it came from the city of Santo Domingo.

The discussion below departs radically from Cochran's revision in rejecting *affinis* while recognizing many other mainland subspecies. In large part this has been due to the much greater amount of material available to us.

Six hundred and fifty-five carefully documented and noted specimens of *A. chrysolaema* have been collected by ourselves and associates between June 1962 and September 1964. Large fresh series of this lizard are now available to us from southern and central Haiti, from Ile de la Tortue and Gonâve, and from the whole of its range in the República Dominicana. These specimens are in the Albert Schwartz Field Series (ASFS) and the collection of Richard Thomas (RT). They have been amassed through the efforts of Miss Patricia A. Heinlein, and Messrs. David C. Leber and Richard Thomas. All deserve our commendations and thanks, most especially Messrs. Leber and Thomas who made special efforts on our behalf to secure topotypes of *A. c. abbotti* on Isla Beata. In addition, we have examined 417 specimens in the following collections: American Museum of Natural History (AMNH), Carnegie Museum (CM), Museum of Comparative Zoology (MCZ), Museum of Zoology, University of Michigan (UMMZ), and United States National Museum (USNM). To the curators and their assistants — Charles M. Bogert and Miss Grace M. Tilger, Neil D. Richmond, Ernest E. Williams, Charles F. Walker and George R. Zug, Doris M. Cochran and James A. Peters — we wish to express our appreciation for allowing us to examine pertinent specimens under their care. Paratypes of new forms have been deposited in the Museum of Natural History, University of Kansas (KU), and the University of Illinois Museum of Natural History (UIMNH), as well as in the above collections. The Harvard collections once again have been indispensable; through the efforts of Dr. Williams, large and well preserved series from northern Haiti have been made available to us; without these our interpretation of the northwestern Haitian situation would have been not merely difficult, but rather impossible. In the matter of literature, Edmond V. Malnate has been most helpful and we are grateful for his cooperation. The illustrations are the work of the junior author.

SYSTEMATIC ACCOUNT

The Species as a Whole

Ameiva chrysolaema may be defined as follows: 1) a large species of the genus *Ameiva* with snout-vent length to 160 mm in males and 134 in females; 2) dorsal caudal scales keeled and straight; 3) ventrals in 10, 11, or 12 transverse rows and in 33 to 41 longitudinal rows; 4) fourth toe subdigital scales from 66 to 101; 5) femoral pores 24 to 52; 6) fifteenth caudal verticil with 30 to 52 scales; 7) dorsal pattern consisting of one of the following: a) a series of dorsal yellow to buffy longitudinal lines on a brown, tan, grayish tan, greenish, or blackish ground color, the lines (straight or wavy) at times modified into dashes, dots, or fused with one another to give ultimately a median dorsal longitudinal band, b) a rather uniform covering of brightly colored (blue, orange, yellow) spots on a dark background, c) a pale ground with dark vermiculations and tigroid vertical lateral bars, or d) completely or almost unicolor dorsally without any striking pattern elements; and 8) hemipenis extending to about the seventh to ninth caudal verticil, sulcate surface naked, sulcus bifurcating apically, the branches ending in two poorly defined scalloped apical discs, non-sulcate surface entirely flounced, the flounces extending to the margins of the sulcate surface, a small smooth triangular area on the non-sulcate side which divides the flounces for about one-third the length of the organ into two fields of flounces which correspond to the apical discs.

The center of the distribution of *A. chrysolaema* is in the Cul de Sac-Valle de Neiba region of Hispaniola; the species is represented by large series and from numerous localities in this general region. From here, *A. chrysolaema* extends westward to the vicinity of Léogâne on the Tiburon Peninsula, and eastward as far as San Pedro de Macorís in the República Dominicana. From Léogâne to San Pedro de Macorís, there is a set of localities which implies a more or less continuous distribution. From this basic center, populations extend northwestward along the shore of the Golfe de la Gonâve into the valley of the Rivière de l'Artibonite, and in the central portion of Haiti at least as far north as the vicinity of Mirebalais. In the República Dominicana, there is practical continuity of the main southern mass of the species north of the Sierra de Neiba in the Valle de San Juan and thence to the Dominico-Haitian border near Pedro Santana and immediately across the border at Cerca-la-Source in Haiti. A second major center lies in the northwestern portion of Haiti and extends thence eastward into the Valle de Cibao in the República Dominicana. Whether these two major populations are completely isolated from one another is unknown; there is at least no contact in the República Dominicana, since the Cordillera Central stands between the two main regions, and the central valley along the eastern slopes of this range is unoccupied by *chrysolaema*.

There are several apparently disjunct populations in southern Haiti and the República Dominicana; in the former country there is a single specimen from Aquin to the west along the Tiburon Peninsula, far removed from the nearest records from Léogâne. In the República Dominicana there are specimens from Juanillo near the eastern extremity of the island. Although there are no records from between San Pedro de Macorís and Juanillo, the species has presumably occurred in that region fairly recently (and may still occur as isolated populations), since it occurs on Isla Catalina and Isla Saona. It is at present unknown from the adjacent mainland in each case. There were two specimens reported (Cochran, 1941:282) from Ile-à-Vache but these cannot now be located; although in two extended visits to this island we secured only the very abundant *A. taeniura* Cope, it is not altogether impossible that *A. chrysolaema* occurs there as well. Finally, there are populations south of the Sierra de Baoruco-Massif de la Selle which are completely cut off by these ranges from their more northern relatives; this same phenomenon has now been noted in several other species of reptiles from this area. These mountains, as well as the virtually non-existent coastal plain along the eastern shore of the Península de Barahona, form an inescapable trap for several reptiles in the southern portion of the Península.

For the remaining satellite islands, *A. chrysolaema* is represented by abundant material from Ile de la Gonâve and occurs also on Ile de la Tortue, Isla Beata, and the Siete Hermanos islands off the northwestern portion of the República Dominicana. Of the three species of Hispaniolan *Ameiva*, none has so broad a range as does *A. chrysolaema*. Nonetheless, there is geographic evidence that even this species is retracting its range; the apparent absence of *chrysolaema* from much of the southeastern portion of the República Dominicana, but its occurrence on off-shore islands in this region, suggests a formerly more widespread distribution in this area.

A. chrysolaema is absent from the distal third of the Tiburon Peninsula in Haiti, and apparently from much of the central portion of that country as well. In the República Dominicana it does not occur in the Cordillera Central nor the Sierra de Neiba, and is absent from the central and eastern portions of the country except along the southeastern coast. Interestingly, despite its occurrence in the Valle de Cibao, it does not occur along the northcentral coast of the República Dominicana. The Cordillera

Septentrional acts as an effective barrier in this region. Much of the eastern República Dominicana is mesic (in fact, the area of highest rainfall in the country occurs in this region), and since *A. chrysolaema* is distinctly a lizard of xeric habitats, this one factor may well have prevented its expansion into this region and onto the Península de Samaná. However, its absence along the coast from Cabo Engaño westward is strange, since this coast is arid and appears suitable for these lizards. Considering the disjunct nature of the populations of the species in extreme eastern Hispaniola, it is possible that it never occurred in this region or that it has already retreated from this suitable coastal area.

A. chrysolaema lives in xeric regions. It is abundant in the Cul-de-Sac plain below sea level and on the Península de Barahona. It occurs also in the dry Valle de San Juan, at elevations of about 1000 feet. Although more tolerant of less xeric situations than *A. lineolata*, the two often occur together, with *A. lineolata* inhibiting more open, cactus-studded, sandy regions, and *A. chrysolaema* preferring slightly more shady areas, such as adjacent copses or thickets of *Acacia*. If lowland woods are present, *A. chrysolaema* may invade them; the woods may not be dense nor with abundant ground cover. Maritime deciduous forests along the mangrove border (but usually not the mangroves themselves) offer a suitable habitat. Scrub-lands and open beaches with some cover are often adequate. In its relationships with the other two species, *A. chrysolaema* most often occurs with *A. lineolata* as noted above. On occasion, however, *A. chrysolaema* occurs with the shade-loving *A. taeniura*. In such instances, *chrysolaema* appears to be the secondary invader of a habitat which is the preferred habitat of *taeniura;* in one such case near Oviedo on the Península de Barahona, *taeniura* kept strictly to the open dry forest, whereas *chrysolaema* occurred almost exclusively along the edges of the woods where they abutted on a dry mangrove flat. The latter is likely the more preferred habitat of *chrysolaema*, but during the heat of the day this species was not averse to foraging in marginal forested situations.

CHARACTERS STUDIED

We have examined a total of 1072 specimens of *A. chrysolaema* (in contrast to 42 examined by Barbour and Noble, 1915, and 198 by Cochran, 1941); of these, 655 are specimens collected by ourselves and parties at various times, and upon which we have extensive data on coloration and pattern. Of the races recognized and described in the present paper, we have seen living or freshly killed specimens of all but two (the race from northwestern Haiti, and the race from extreme eastern República Dominicana). We feel that data on coloration and pattern are absolutely indispensable for any modern worker on the genus *Ameiva*. Old, faded, or (even worse) badly discolored specimens are completely useless except for scale counts and measurements, and analyses of populations must rest heavily and securely upon data from living or freshly killed animals.

We have taken counts of rows of longitudinal and transverse ventrals, fourth toe subdigital scales, femoral pores, and scales in the fifteenth tail verticil (see Tables 1-4). Of these, only the number of transverse rows of ventrals can be used (partially) to characterize subspecies — i.e., having either 10 or 12 transverse rows of ventrals. No population has all specimens with 10 or all with 12 rows. However, there is most often a preponderance of one or the other in any particular sample, and we have used this modal number as typical of the race in question (Table 2), unless the sample is rather small or the two categories differ by only a very few individuals.

Of least value systematically is the number of longitudinal rows of ventrals. In the entire lot of *A. chrysolaema* examined, this figure varies from 33 to 41. The means for the 15 populations described herein vary from 38.3 to 36.5. Data for longitudinal rows are presented in each case, but these data are not emphasized.

The counts of fourth toe scales, femoral pores, and fifteenth verticil scales show some trends, although in almost all cases the amount of overlap is rather large between most populations. Differences of means, however, between those races which rank first and last in each category may be rather striking (see Tables 2, 3 and 4). The largest difference between the highest and lowest populations is in fourth toe scales, where the high population has a mean of 91.0, and the low 77.8 — a difference of 13.2 scales. For facility we have combined in all cases the fourth toe scales from both feet and the femoral pore counts for both legs into one figure for each specimen; we do not feel that this weakens the use of the data and it may well intensify slight differences, which would otherwise be almost unnoticeable. We have given the means and extremes for these three scale counts for each subspecies; the differences, if any, obviously are mean differences, since overlap of ranges is great in most cases.

THE RECOGNIZABLE SUBSPECIES

AMEIVA CHRYSOLAEMA CHRYSOLAEMA Cope, 1868

Ameiva chrysolaema Cope, 1868, Proc. Acad. Nat. Sci. Philadelphia, 20:127 (type locality — ''Ile de la Gonâve'' = within 25 miles of Port-au-Prince, *fide* Cochran, 1941:275).

Ameiva vittipunctata Cope, 1871, Proc. Acad. Nat. Sci. Philadelphia, 22:220 (type locality — ''city of Santo Domingo'' = within 25 miles of Port-au-Prince; see Cochran, 1941:275-76 for discussion of rationale for this restriction).

Ameiva affinis Fischer, 1883, Beschreibungen neuer Reptilien, [Separat-Abdruk aus dem] Osterprogramm des akademischen Gymnasiums, Hamburg, p. 1 (type locality — ''Haiti'').

Diagnosis: A subspecies of *A. chrysolaema* characterized by a combination of very large size (males to 160 mm, females to 130 mm snout-vent length), usually 12 transverse rows of ventrals, moderate number of fourth toe subdigital scales, high number of femoral pores and of scales in the fifteenth tail verticil; dorsal pattern consisting of about six longitudinal yellow lines and/or yellow dots arranged in series (Fig. 1, *left*), and a black gular band which may involve the chest and undersides of the arms.

Distribution: From St. Marc (and including the ''Artibonite Valley'') on the north, southeast along the shore of the Golfe de la Gonâve, east throughout the Cul-de-Sac plain to the environs of Etang Saumâtre (Manneville, Gauthier, Fond Parisien), and west on the Tiburon Peninsula as far as the vicinity of Léogâne (Père); an isolated specimen from Aquin, Dépt. du Sud, Haiti (Fig. 11).

Discussion: A. c. chrysolaema is distinctly the largest and most bulky of the races of the species. Males reach a snout-vent length of 160 mm and females 130 mm. Color notes on a series from Eaux Gaillées in the Haitian Cul de Sac show the situation as far as coloration and pattern are concerned. Males from Eaux Gaillées were noted as dark brown to reddish brown dorsally, especially reddish on the shoulders and head (which may also be grayish). Lores and cheeks with gray blotches. The back has either a series of six yellow lines and yellow dots in the interspaces between the lines, or has six rows of lemon yellow spots. The lateral fields are black with or without a longitudinal series of yellow spots. The lower sides have large yellow spots as well, and the lateralmost belly plates are blue-spotted. The ventral ground color is dull blue-gray, the throat pale orange (Maerz and Paul, 1950, Pl. 9D7). There is a black gular band,

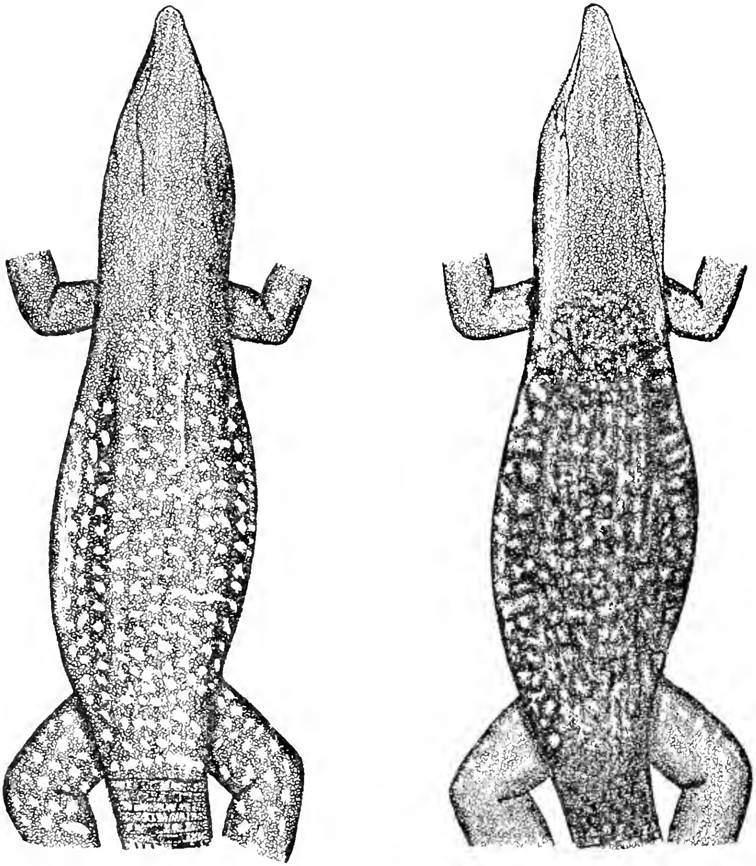

Fig. 1. *Left, Ameiva chrysolaema chrysolaema,* ASFS X2162, 3.9 mi. NW Ganthier, Dépt. de l'Ouest, Haiti. *Right, Ameiva c. umbratilis,* holotype, MCZ 77231, Barahona, Barahona Prov., República Dominicana.

which may expand posteriorly to cover the chest and undersides of the arms. Some adult males have the shoulders and neck blackened, so that in these regions the yellow lines are much dulled and obscured. The females are like the males except that the lines are yellow and prominent anteriorly. The venter is dull blue-gray. The black gular collar is present but less pronounced than that of the males, and the throat is orange but paler than that of males.

A series from Diquini to the west of Port-au-Prince was colored much as the Eaux Gaillées material. The dorsal ground color in males was brown with yellow dots arranged in lines or with yellow lines additionally present. There is a black lateral field with yellow spots. The sides of the head and axillae had vivid and prominent blue to blue-green blotches. The heads were dull reddish brown to dull orange, with orange-pink throats. The ventral ground color was grayish to orange with blue spots on the sides of the abdomen. The hindlimbs were dotted with yellow, the forelimbs with blue-green. Females resemble the males, but the dorsal lines or dots are less bright and prominent.

From the above descriptions it is obvious that, despite some differences in details, these two populations (as well as many others throughout the range of *chrysolaema*) share a community of dorsal markings — the longitudinal series of yellow lines and/or dots. Cochran (1941: pl. 8E) showed a dorsal view of the type of *A. chrysolaema*. The six dorsal lines, in this case partially fragmented into series of longitudinal dashes, are quite distinct. There is no doubt that the type of *A. chrysolaema* did indeed originate in the vicinity of Port-au-Prince, since only this subspecies occurs anywhere near that city. Specimens from Ile de la Gonâve are much duller, less prominently marked, lack fragmentation of the dorsal lines, and are not referable to the nominate form.

The longitudinal ventrals vary between 35 and 40 (mean 37.7) and these scales are most often arranged in 12 transverse rows (67.9 per cent), with 29.2 per cent having 10 transverse rows and 2.9 per cent having 11 rows. The variation in number of transverse rows depends primarily on whether the lateralmost of the enlarged ventral scales is sufficiently large to be considered a ventral; we have so considered it if its length (longitudinally) is equal to that of the next inner adjacent row, and if its width (transversely) is equal to at least half that of the next inner adjacent row. Occasional specimens may also have one or two rows of the belly plates divided, thus attaining counts of 11 or 12 in another fashion.

The fourth toe subdigital scales range from 76 to 101 (mean 86.7) and the femoral pores range from 33 to 50 (mean 43.7). The scales in the fifteenth caudal verticil vary between 37 and 51 (mean 44.4).

Within the range ascribed to *A. c. chrysolaema*, there are various relatively minor pattern variants which we consider as part of the normal variation of the subspecies. Specimens from St. Marc at the northwesternmost extreme of the range are very boldly lined longitudinally; the same is true of two individuals from Manneville. In both cases there are specimens from adjacent localities or from the same locality which have more typical *chrysolaema* markings.

The single individual from Aquin (USNM 72614) is unique in several (possibly significant) features. The longitudinal lines are composed of dots which also have a more or less transverse arrangement, so that the back has a rather conspicuous transversely banded appearance, a condition seen in no other *A. c. chrysolaema*. The black lateral field is obscured, and there is no black gular band, the entire throat, chest and undersides of the arms being unmarked. The specimen is an adult male with a snout-vent length of 146 mm, ventrals in 38 longitudinal and 12 transverse rows, 95 subdigital fourth toe scales, 41 femoral pores, and 43 scales in the fifteenth caudal verticil. None of these counts will distinguish the specimen from *A. c. chrysolaema,* although we attach no particular significance to this fact. Considering the wide gap between the known localities of *A. chrysolaema* between Père near Léogane and Aquin (a distance of some 90 kilometers) and the fact that the Aquin specimen comes from the southern, in contrast to the northern, side of the Tiburon Peninsula, it is likely that this single individual comes from a population which is distinct from *A. c. chrysolaema.* Without additional material, and especially lacking careful data on coloration and pattern in life, we are unwilling to name this single Aquin specimen as distinct from *A. c. chrysolaema.*

The character ascribed by Cochran (1941:277) to differentiate *A. c. affinis* — i.e., the interparietal being larger than the adjacent scales — we find to be completely untenable. Dr. Cochran has also shown (1941:291) that the scale counts of *affinis* fall within the known range of *A. c. chrysolaema.* Specimens which she assigned to *affinis* were reported (1941:292) from Momance, Manneville, and Père in Haiti. Other specimens (p. 282) from Manneville were assigned to *c. chrysolaema.* In a series of twenty-seven specimens from Fond Parisien and the eastern Cul de Sac, for example, six have the interparietal larger than adjacent scales and the balance have the interparietal smaller. The same situation applies to series from other localities within the range of *A. c. chrysolaema,* and if we accept *affinis* as differentiated by this character alone, then the races *chrysolaema* and *affinis* are broadly and randomly sympatric. No features of pattern or coloration will distinguish specimens with smaller interparietals from those with larger interparietals, and we cannot detect any other constant scale feature which will distinguish two forms in this region. For this reason we consider *affinis* Fischer as a synonym of *chrysolaema* Cope. The reasons for considering *vittipunctata* Cope as a synonym of *chrysolaema* have been outlined in the introduction.

Specimens examined: Haiti, Dépt. de l'Artibonite, "Artibonite Valley" (not mapped), 1 (USNM 75921); St. Marc, 5 (USNM 59079, MCZ 58012-13, 65351, AMNH 49766); *Dépt. de l'Ouest,* 2.2 mi. (3.5 km) SW Trou Forban, 1 (ASFS X1927); between Arcahaie and Trou Forban, 1 (MCZ 51433); 6.3 mi. (10.1 km) NE Arcahaie, 3 (ASFS X1928, X1930, X1946); 13 mi. (20.8 km) SW Arcahaie, 1 (ASFS X1938); Port-au-Prince, 12 (AMNH 49637-38, MCZ 13839, 59495-502, 69420); Carrefour Feuille, Port-au-Prince (not mapped), 1 (MCZ 65810); Delmas, 2 (MCZ 65808-09); Pétionville, 1 (USNM 59078); 10 mi. (16 km) SW Port-au-Prince, 1 (UMMZ 92197); 3.5 mi. (5.6 km) E Croix des Bouquets, 15 (ASFS X2197-211); Eaux Gaillées, 33 (ASFS X1651-83); Manneville, 11 (MCZ 8621-23, 8625, 8629-33, 8614, 8618); 3.9 mi. NW Ganthier, 18 (ASFS X2153-70); 1.3 mi. (2.1 km) NW Fond Parisien, 3 (ASFS X2174-76); 0.4 mi. (0.6 km) SE Fond Parisien, 7 (ASFS X2189-95); Hatte Latham (not mapped), 1 (MCZ 51424); Diquini, 36 (ASFS X2381-407, MCZ 6292, 8706, 8649-51, 8653-54, 8658-59); Momance, 8 (MCZ 8634-35, 8638-41, 8649, 20875); Ça Ira, 2 (MCZ 64919-20); Père, 3 (MCZ 13271-73); *Dépt. du Sud,* Aquin, 1 (USNM 72614).

AMEIVA CHRYSOLAEMA UMBRATILIS,[1] new subspecies

Holotype: MCZ 77231, a subadult female, from Barahona, Barahona Province, República Dominicana, taken 25 July 1963, one of a series taken by native collectors. Original number X9721.

Paratypes: All from the República Dominicana, as follows: MCZ 81000-04, USNM 152558-60, KU 79861-64, UIMNH 56886-89, RT 738-39, same data as holotype; ASFS X9568-69, Barahona, Barahona Prov., 24 July 1963, native collector; AMNH 37943-49, 38133-39, Barahona, Barahona Prov., 12 October 1922,

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[1] From the Latin for "remaining in the shade."

G. K. Noble; AMNH 63191, 63193, Barahona, Barahona Province, 10-19 July 1932, W. G. Hassler; MCZ 58019, Barahona, Barahona Prov., 13 July 1932, W. G. Hassler; MCZ 43813-14, Barahona, Barahona Prov., 18 July 1932, W. G. Hassler; ASFS V199-200, 4 km NW, 1 km SW Barahona, Barahona Prov., 5 August 1963, A. Schwartz, R. Thomas; AMNH 49837-38, "Palomino Springs, nr. Barahona" (not mapped), Barahona Prov., 15 August 1935, W. G. Hassler.

Associated specimens: República Dominicana: Independencia Prov., 6.5 mi. (10.5 km) NE Jimaní, 1 (ASFS X9507); 4.4 mi. (7.0 km) SE Jimaní, 3 (ASFS X9515-17); 13 km SW La Descubierta, 3 (ASFS X9364-66); 5 km E La Descubierta, 5 (ASFS X9354-58); Las Baitoas, 1 (MCZ 58776); 22 km SE Duvergé, 7 (ASFS X9928-34); 1 km W El Naranjo, 1000 feet, 2 (ASFS X9943-44); northwest side, Laguna del Rincón, 1 (MCZ 58779); Guayabal, 9 km N Postrer Río, 2 (MCZ 57732-33); *Baoruco Prov.*, Jaragua, 5 (ASFS X9469-72, RT 713); 0.7 mi. (1.2 km) E El Estero, 2 (ASFS X9467-68); 0.8 mi. (1.3 km) SW Neiba, 15 (ASFS V252-64, RT 775-76).

Diagnosis: A subspecies of *A. chrysolaema* characterized by a combination of moderate size (males to 130 mm, females to 112 mm snout-vent length), usually 10 (but often 12) transverse rows of ventrals, moderate number of fourth toe subdigital scales, low number of femoral pores, and high number of scales in the fifteenth caudal verticil; dorsal pattern consisting of dull grayish brown to greenish black dorsal ground color with a series of eight to ten dorsal longitudinal lines composed of small and numerous dull yellowish to tan dots (Fig. 1, *right*), and a black gular band which in adult males may involve the chest and undersides of the arms.

Distribution: The Valle de Neiba from just east of Jimaní to the vicinity of the city of Barahona, República Dominicana (Fig. 11).

Description of type: A subadult female with the following measurements and counts: snout-vent length 93 mm, tail 184 mm; ventrals in 37 longitudinal and 10 transverse rows; fourth toe subdigital scales 39 and 41 (total 80); femoral pores 18 and 17 (total 35); 43 scales in the fifteenth caudal verticil. Dorsal ground color grayish brown in life, head gray, shoulders greenish; ten rows of dull yellowish dorsal dots, the dots in each series virtually confluent with one another, giving a vague wavy line; lateral fields obscure darker gray with scattered buffy dots.

Throat pale purplish orange, followed by a black gular band which extends slightly onto the chest and onto the underside of the forelimbs; ventral ground color grayish blue; tail dull grayish brown above and grayish blue below, with some scattered darker scales dorsally.

Variation: See tables. The characters of *umbratilis* are best expressed in populations from the eastern section of the Valle de Neiba; however, even the most western specimens from the vicinity of Jimaní are in no way comparable to Haitian *A. c. chrysolaema.* The dorsal ground color was noted in life as being greenish black (Jimaní, La Descubierta, Jaragua), greenish brown (Duvergé, El Naranjo), brown (El Estero), and grayish brown (Barahona). The dots in the dorsal longitudinal lines are tiny and very often confluent, giving almost a vermiculate appearance to the dorsal band; the dots vary in color from greenish (Jimaní), creamy (La Descubierta), pale yellow to pale green (Duvergé), yellow (El Estero), grayish yellow (Jaragua). or dull yellowish to tan (Barahona).

The lateral fields are usually dull and inconspicuous, hardly darker than the lateral coloration; they often include a row of yellow to creamy spots and are not outlined either above or below by pale and prominent longitudinal lines. The ventral coloration varies from pinkish gray and grayish orange to grayish blue, with specimens having the brighter colors known from the western extremity of the range. The throats are dull pinkish gray and grayish orange to dull purplish or dull orange. The black gular band is invariably present and may, in adult males, expand to cover much of the chest and anterior abdomen and underside of the forelimbs. The upper surfaces of the limbs are usually unspotted, but if there are a few scattered dots these are blue on the forelimbs and yellow on the hindlimbs.

Comparisons: The coloration and pattern of *chrysolaema* and *umbratilis* are strikingly different; even in the western portion of the range of *umbratilis*, no specimen approaches closely the vivid dorsal coloration and pattern of the nominate race. The extreme condition in the eastern Valle de Neiba contrasts strongly with the condition at Fond Parisien, for instance, and specimens from Jimaní and La Descubierta are much more like individuals from Barahona in having fine dorsal dotting and generally more drab colors than they are to specimens from Fond Parisien. *Umbratilis* is a smaller lizard; no specimen of either sex of this race achieves the much bulkier and larger size of *chrysolaema.* This is certainly not a sample artifact since large series of both forms are at hand. The tendency for *umbratilis* to have 10 versus 12 transverse rows of ventrals, as in *chrysolaema,* is of interest, although in *umbratilis* the specimens are almost equally divided between the 10- and 12-row conditions. In number of longitudinal ventral rows, the two races are comparable (*chrysolaema* 37.7, *umbratilis* 37.1). In number of femoral pores these two races differ strongly, with a mean of 43.7 in *chrysolaema* and 35.6 in *umbratilis. Chrysolaema* averages slightly higher in counts of femoral pores and fifteenth verticil scales.

Remarks: The occurrence of two very distinct races of *A. chrysolaema* in the Cul de Sac-Valle de Neiba complex is surprising. Aside from the more mesic eastern and western ends of this long xeric valley, the conditions throughout are quite comparably severe. Interestingly, the Valle de Neiba is greatly constricted just to the east of Jimaní; it is possible that this narrow neck (7-10 km) has been effective in separating these two races. Specimens from the República Dominicana to the northwest of Jimaní may well be assignable to *A. c. chrysolaema.*

AMEIVA CHRYSOLAEMA BOEKERI Mertens, 1938

Ameiva chrysolaema boekeri Mertens, 1938, Senckenbergiana, 20:338 (type locality — south of Fondo Negro, lower Río Yaque del Sur, Barahona Province, República Dominicana).

Diagnosis: A subspecies of *A. chrysolaema* characterized by a combination of moderate size (males to 126 mm, females to 111 mm snout-vent length), usually 10 transverse rows of ventrals, moderate number of fourth toe subdigital scales, low number of femoral pores, and high number of scales in the fifteenth verticil; dorsal pattern of two phases: (1) back yellowish brown, grayish tan, to olive, and without pattern and often without any indication of lateral fields, or (2) dorsum colored as above but with faint paler marblings or longitudinal lines and a fairly prominent black to dark gray lateral field (Fig. 2), and a black gular band which may involve the chest and underside of the arms.

Distribution: North of the Río Yaque del Sur in extreme eastern Valle de Neiba, north and east to north of Azua and east to the vicinity of Baní, in the Llanos de Azua, República Dominicana; intergrades with the next subspecies to the northwest in the vicinity of Hato Nuevo, Azua Province (Fig. 11).

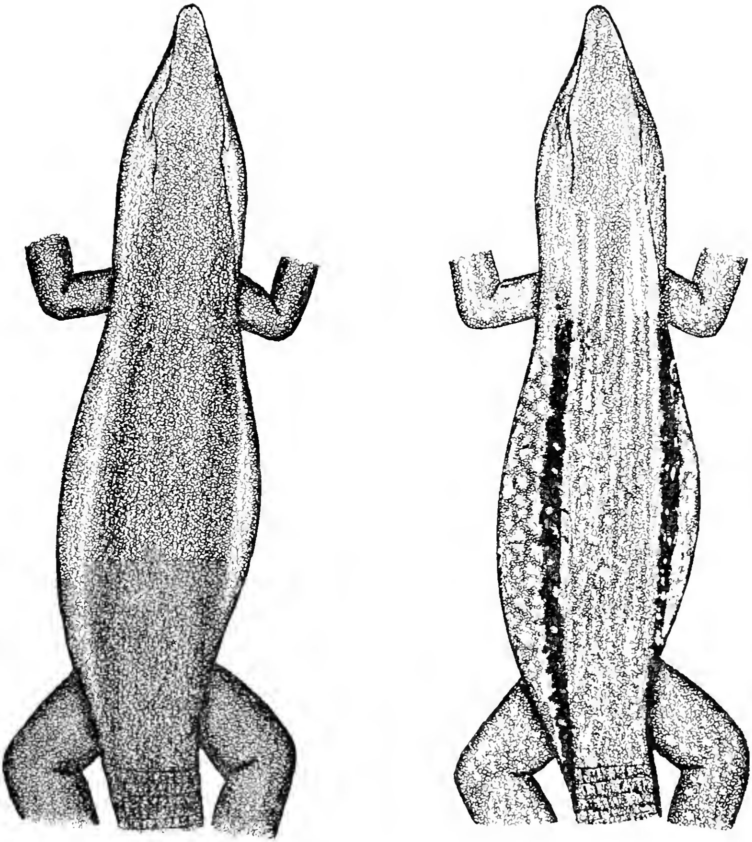

Fig. 2. *Left, Ameiva c. boekeri*, ASFS X7811, 10 mi. NW Baní, Peravia Prov., República Dominicana. *Right, Ameiva c. boekeri*, ASFS V689, 15.2 mi. S San José de Ocoa, Peravia Prov., República Dominicana.

Discussion: A. c. boekeri was described on the basis of fourteen lizards from Fondo Negro. Of these, seven males were dorsally patternless (including the type), four males showed a "*chrysolaema*"-like pattern, and the final male was considered by Mertens (1939:72) to resemble the Beata race *abbotti* — i.e., it was dorsally dotted. The two paratypic females were "*chrysolaema*"-like as well. We have examined a single paratype of *boekeri* (MCZ 44757) and eighty-six other specimens from the range ascribed by us to *boekeri* above. Of ten localities, only two have "pure" or almost "pure" *boekeri* populations (i.e., patternless), viz., a series of five specimens from the west side of Punta Martín García, Barahona Province, and a series of twenty-one from 10 mi. NW Baní, Peravia Province. Additional specimens (four) from the eastern side of Punta Martín García show the typical duality of dorsal pattern, however, and thus the uniformity of this small series of five is not significant. The large series from Baní, on the other hand, has only a single adult male which shows any pattern; this population is thus almost completely patternless. A fresh series of five topotypes from Fondo Negro has four individuals with patterns, and one without pattern. Thus, although the patternless condition predominates at some localities (Baní), elsewhere (and including the type locality) both types of dorsal pattern occur.

The two types of dorsal patterns, as delimited by Mertens, grade into one another. The back may be longitudinally lined with from six to ten tan to yellowish lines of fine dots, or these may be very obscure centrally and more prominent at the sides of the dorsal field. Some individuals have the back finely marbled. The lateral fields are well developed and enclose a series of buffy to cream dots; the lateral fields are often outlined below by a longitudinal yellowish line, and a similar line may border these fields above. The lower sides may be dotted with blue or bluish green. The dotted condition of the back, considered by Mertens as being *abbotti*-like, is not at all comparable to the large and brilliant sky-blue spotting on a black ground of that race. There is some similarity between patterned *boekeri* and *umbratilis*. No *umbratilis* however is unpatterned.

In patternless lizards, the dorsal ground color was recorded as yellowish brown (Fondo Negro), brown (San José de Ocoa), grayish tan (Punta Martín García), black (Barreras), and reddish brown (Baní). The lateral fields may be completely absent or may be indicated by a somewhat grayer longitudinal lateral stripe, without any sort of included or adjacent pale dots. The ventral ground color is blue-gray, purplish blue, blue, light olive, gray, or orange-gray. The throat is likewise variable, but is some shade of dull orange; females have throats which are typically more grayish orange than males. The tails are brown to grayish tan above, and gray below.

Scale counts for the series (including intergrades from Hato Nuevo) are: longitudinal ventrals 34-40 (mean 37.2), transverse ventrals in 10 (82.4 per cent) or 12 (17.6 per cent) rows, fourth toe scales 73 to 98 (mean 84.6), femoral pores 31-41 (36.5), fifteenth verticil 37-48 (mean 42.7).

The much smaller size and faded pattern of those *boekeri* which have patterns, as well as the patternless individuals, can easily be distinguished from *A. c. chrysolaema*. *Chrysolaema* is likewise characterized by 12 rather than 10 rows of ventrals. In counts of fourth toe scales, femoral pores, and fifteenth verticil scales, *boekeri* averages less than *chrysolaema*, the most striking difference being in femoral pores (*chrysolaema* 43.7, *boekeri* 36.5). Patternless *boekeri* can be easily differentiated from all *umbratilis*, since this race is never patternless. Patterned *boekeri* are much like *umbratilis*. In both, the dorsal pattern is faded and not well demonstrated. One feature is suggestive; patterned *boekeri* have the lateral fields prominent and often outlined both above and below, whereas the typical *umbratilis* condition is an obscure lateral field, not set off by longitudinal pale lines. Both *umbratilis* and *boekeri* usually have 10 rows of ventrals, although *umbratilis* has a much higher frequency of 12-row individuals. In counts of fourth toe scales and femoral pores, *boekeri* averages slightly higher than *umbratilis;* the means for fifteenth verticil scales are identical.

Because of the similarities of *umbratilis* and patterned *boekeri*, we have considered the possibility that the name *boekeri* should be applied to *Ameiva* from the Valle de Neiba. To be counted against this conception is the fact that of 61 *umbratilis*, none is unpatterned, whereas 56.3 per cent of the specimens (*boekeri*) from north of the Río Yaque del Sur are patternless. There is no indication of this patternless condition in specimens from Barahona, nor from elsewhere in the range of *umbratilis*. We prefer to regard *boekeri* as a separate entity, distinct from *umbratilis* to the south.

A. c. boekeri is approached geographically by three adjacent races; of these it is known to intergrade only with the race to the northwest in the Valle de San Juan (these intergrades will be discussed later). From *umbratilis* the range of *boekeri* is separated by the lower reaches of the Río Yaque del Sur and by the extremely mesic conditions of much of the eastern portion of the Valle de Neiba. Although *boekeri* is not presently known to intergrade with the race next to the east along the southern coast of the República Dominicana, it may well do so. It is certainly significant that *boekeri* occupies the western Llanos de

Azua in the vicinity of Baní; just to the east of that city, conditions become more mesic, and the region is occupied by another race. Intergradation likely takes place where these two regions come into contact.

Specimens examined: República Dominicana, Barahona Prov., Fondo Negro, 6 (ASFS X9703-07, MCZ 44757); west side, Punta Martín García, 5 (ASFS V84-88); *Azua Prov.,* 3 km E Barreras, 2 (ASFS V3164-65); 2 km W Puerto Viejo, 2 (ASFS V3183-84); 22 km NW Azua, 3 (ASFS V465-67); 1.8 mi. (2.9 km) W, 1.1 mi. (1.8 km) N Azua, 18 (ASFS X8002-18, X8103); 1.8 mi. (2.9 km) W, 2.7 mi. (4.3 km) N Azua, 10 (ASFS X8019-28); *Peravia Prov.,* 8.9 mi. (13.9 km) S San José de Ocoa, 1300 feet (430 m), 1 (ASFS V714); 15.2 mi. (24.3 km) S San José de Ocoa, 9 (ASFS V687-95); 10 mi. (16 km) NW Baní, 23 (ASFS X7801-21, RT 613-14). Intergrades between *A. c. boekeri* and the race to the northwest were examined from: *República Dominicana, Azua Prov.,* Hato Nuevo, 10 (ASFS X437-46).

AMEIVA CHRYSOLAEMA ALACRIS,[1] new subspecies

Holotype: MCZ 77232, an adult male, from 10 km SE San Juan, San Juan Province, República Dominicana, one of a series taken 9 August 1963 by Albert Schwartz and Richard Thomas. Original number V283.

Paratypes: All from the República Dominicana, as follows: ASFS V284-97, same data as holotype; RT 778-79, 10 km S San Juan, San Juan Prov., 9 August 1963, R. Thomas; MCZ 81005-06, USNM 152561-64, AMNH 92842-43, KU 79865-66, UIMNH 56890-93, 2.5 km W, 4.4 km S San Juan, San Juan Prov., 9 August 1963, D. C. Leber, R. F. Klinikowski; KU 79867-68, AMNH 92844, 2.5 km W, 5.4 km S San Juan, 9 August 1963, D. C. Leber, R. F. Klinikowski; ASFS V389-90, 10 km E Vallejuelo, San Juan Prov., 12 August 1963, R. Thomas; USNM 152565, 3 km E Las Matas, San Juan Prov., 9 August 1963, R. Thomas.

Associated specimens: Haiti, Dépt. du Nord, Cerca-la-Source, 1 (USNM 76780); *República Dominicana, San Rafael Prov.,* 3.8 mi. (6.1 km) SE Sabana Cruz, 1 (ASFS V329); Guayabal, 1 (MCZ 58672); *Azua Prov.,* Túbano (= Padre las Casas), 3 (USNM 66729-31); 0.7 mi. (1.1 km) NW Villarpando, 9 (ASFS V419-27).

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[1] From the Latin for "lively."

Diagnosis: A subspecies of *A. chrysolaema* characterized by a combination of moderate size (males to 126 mm, females to 109 mm snout-vent length), usually 10 transverse rows of ventrals, moderate number of fourth toe subdigital scales, very low number of femoral pores, and high number of scales in fifteenth caudal verticil; dorsal pattern consisting of five to seven bold longitudinal dorsal lines (the lateralmost forming a strong upper border to the prominent black lateral fields with their enclosed bright yellow dots), the longitudinal lines never broken into dots and lines as in *c. chrysolaema* and always conspicuous and discrete (Fig. 3, *left*), and a black gular band which rarely involves also the chest and undersides of the arms.

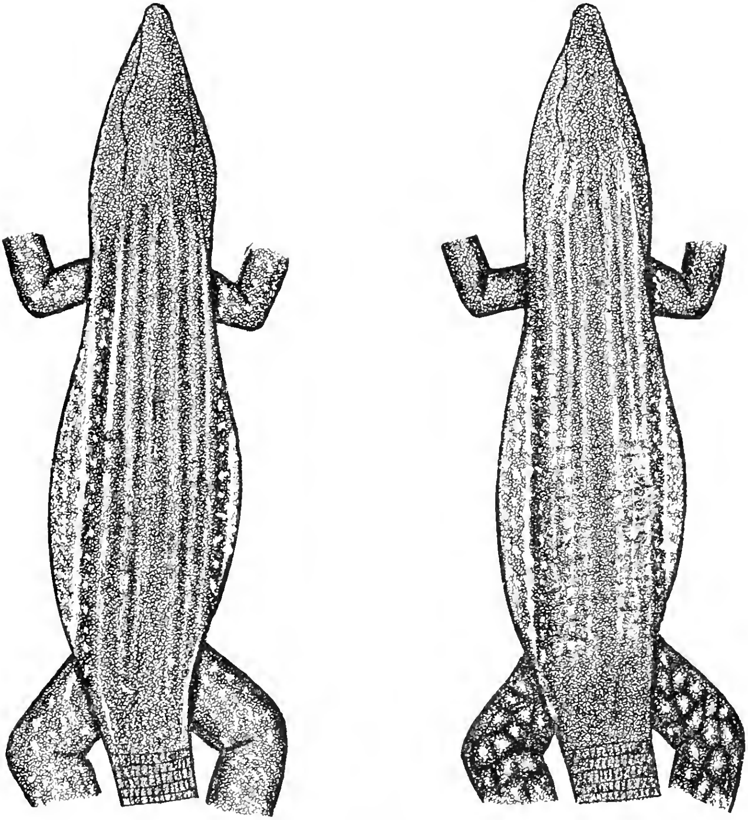

Fig. 3. *Left*, *Ameiva c. alacris*, holotype, MCZ 77232, 10 km SE San Juan, San Juan Prov., Republica Dominicana. *Right*, *Ameiva c. procax*, holotype, MCZ 77233, Santo Domingo, 2.2 km SW Río Ozama, Dist. Nac., República Dominicana.

Distribution: From east central Haiti (Cerca-la-Source) southeastward through the Valle de San Juan (Fig. 11); intergrading with *A. c. boekeri* at Hato Nuevo, Azua Province, and with *A. c. chrysolaema* in the vicinity of Mirebalais, Dépt. de l'Ouest, Haiti (see discussion below).

Description of type: An adult male with the following measurements and counts: snout-vent length 116 mm, tail 200 mm; ventrals in 37 longitudinal and 12 transverse rows; fourth toe subdigital scales 42 and 44 (total 86); femoral pores 16 and 16 (total 32); 46 scales in the fifteenth caudal verticil. Dorsal ground color brown with seven longitudinal pale yellow lines, the lateralmost bordering above the black lateral fields with their isolated yellow dots; lateral fields bordered below by a slightly duller longitudinal line which contains a series of bright yellow dots; lower sides dotted with yellow. Throat gray, venter dull, dirty orange. A black gular band, not extending onto the chest or undersides of the arms. Tail brown above, gray below, with an indistinct proximal and lateral area of yellowish dots; top of tail with some darker brown scales. Fore- and hindlimbs with pale scattered small dots, bluish on forelimbs and yellowish on hindlimbs.

Variation: See tables. *A. c. alacris* presents a constant assemblage of coloration and pattern elements throughout its range. The dorsal ground color is always brown, with from five to seven pale or dull yellow longitudinal lines, these lines always forming a conspicuous pattern. The lines are entire and not fragmented or modified into series of longitudinal dots, although in some specimens the more central lines, especially posteriorly, may be broken into dashes. In general, however, the integrity of the lines (even when fragmented) is maintained. The black lateral fields are bold, set off by pale longitudinal lines above and below, and enclose a single series of scattered yellow dots; the lower line bordering the lateral field may have superimposed upon it a series of bright yellow dots, thus rendering the black lateral field even more conspicuous. The lower sides are dotted with yellow. The throat varies from gray to very pale orange, and the venter likewise varies between these two extremes.

A. c. alacris intergrades to the southeast with *A. c. boekeri* and to the southwest with *A. c. chrysolaema*. A series of ten specimens from Hato Nuevo, Azua Province (ASFS V437-46), shows the intergradation with *boekeri*. Of this series, five are unpatterned *boekeri*, and five represent the patterned phase of that race. These five patterned lizards have the lateral fields darker than most patterned *boekeri*, and there is a distinct tendency to have the dorsal lines more boldly (brighter yellow) displayed anteriorly, although the posterior dorsal pattern is fainter and very like "typical" patterned *boekeri*. The distance from Hato Nuevo (*alacris* X *boekeri* intergrades) to Villarpando (*alacris*) is only ten kilometers, yet the series from the latter locality is typical of *alacris* in all ways and has no patternless individuals.

From the vicinity of Mirebalais, Dépt. de l'Ouest, Haiti, we have examined specimens from the following localities: 3.4 mi. (5.4 km) NE Barrage de Peligre, 2 (ASFS X2217-18); 1.1 mi. (1.8 km) S Mirebalais, 3 (ASFS X2237-39); Mirebalais, 1 (MCZ 68510); La Tombe, nr. Mirebalais, 8 (MCZ 68517-24); Boudou, nr. Mirebalais, 2 (MCZ 69387-88); Duvié, nr. Mirebalais, 1 (MCZ 68478). Of these, the last three places named, La Tombe, Boudou, and Duvié, cannot be located; they have not been mapped. Taken as a whole, this lot of lizards is intermediate between *chrysolaema* and *alacris*, although they are closer to *alacris* than to *chrysolaema*. Three lizards (ASFS X2237, ASFS X2217, MCZ 68510) show the disintegration of the dorsal lines into series of yellow spots, a typical *chrysolaema* feature. Several male specimens are larger than *alacris*, with snout-vent lengths of 133 to 145 mm (five lizards); two females have snout-vent lengths of 109 mm (the upper extreme of *alacris* females), and another has a snout-vent length of 110. In life, our specimens from Barrage de Peligre and Mirebalais had yellow lines and a greenish wash on the neck — the latter a *chrysolaema* character. Finally, some individuals have a discrete black gular band as in *alacris*, whereas others have the band expanded onto the chest and arms as in *chrysolaema*. We consider this entire lot of specimens intergradient between *alacris* and *chrysolaema*.

Comparisons: A. c. alacris is easily distinguished from the three previously described races on the basis of dorsal pattern; the discrete, bold, and undotted longitudinal lines of *alacris* contrast with the patternless or weakly patterned races *boekeri* and *umbratilis*, and with the larger and dorsally dotted and lined *chrysolaema*. *Alacris* is a race with ten transverse rows of ventrals as are *umbratilis* and *boekeri*, in contrast to the twelve-rowed *chrysolaema*. In fourth toe scales, *alacris* (84.8) averages close to *boekeri* (84.6), slightly higher than *umbratilis* (83.0) and lower than *chrysolaema* (86.7). In femoral pores, *alacris* has the lowest average (33.8) of any race of *A. chrysolaema;* of the described forms, it is approached by *umbratilis* (35.6) and *boekeri* (36.5) and is far below *chrysolaema* (43.7). In scales in the fifteenth caudal verticil, on the other hand, both *alacris* and *chrysolaema* are high (44.0 and 44.4), with *boekeri* and *umbratilis* (both 42.7) lower.

Remarks: A. c. alacris occupies the high and xeric Valle de San Juan and associated upland foothills (i.e., Túbano). It is likely that it is more widespread in east-central Haiti than the present evidence of one specimen from Cerca-la-Source indicates. Presumably the race follows down the valley of the Rivière de l'Artibonite, and in the vicinity of Mirebalais has genetic contact with the more southern *chrysolaema*. Such genetic continuity may come across the Montagnes de Trou d'Eau from the Cul de Sac (although there is no obvious means of penetration of this mountain mass), or *chrysolaema* may reach Mirebalais via the valley of the Artibonite from the St. Marc area. The only evidence for the latter is the single specimen noted under *A. c. chrysolaema* from the "Artibonite Valley"; this individual may have come from some undetermined locality which is intermediate between St. Marc and Mirebalais. Further collecting in these areas should easily reveal the precise place of contact between these two races.

AMEIVA CHRYSOLAEMA PROCAX[1] new subspecies

Holotype: MCZ 77233, an adult male, from Santo Domingo, 2.2 km SW of the Río Ozama, Distrito Nacional, República Dominicana, one of a series taken 14 June 1963 by Ronald F. Klinikowski, David C. Leber, and Richard Thomas. Original number X7714.

Paratypes: All from the República Dominicana, as follows: ASFS X7711-13, X7724-26, MCZ 81007-10, USNM 152566-70, KU 79869-71, UIMNH 56894-97, RT 605-08, same data as holotype; ASFS X9254-56, Santo Domingo, old airport, Distrito Nacional, 17 July 1963, D. C. Leber, R. Thomas; AMNH 92845-49, 5.9 km W Santo Domingo, Distrito Nacional, 20 June 1964, D. C. Leber, R. Thomas.

Associated specimens: República Dominicana, San Cristóbal Prov., 8.4 mi. (13.6 km) NE Sabana Grande de Palenque, 2

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[1] From the Latin for "bold."

(ASFS X8167-68); 4.2 mi. (6.7 km) NE Sabana Grande de Palenque, 22 (ASFS X8149-66, RT 643-46).

Diagnosis: A subspecies of *A. chrysolaema* characterized by a combination of large size (males to 141 mm, females to 116 mm snout-vent length), usually 10 (but often 12) transverse rows of ventrals, moderate number of fourth toe subdigital scales, low number of femoral pores, and high number of scales in the fifteenth caudal verticil; dorsal pattern a series of six or seven longitudinal yellow lines in a reddish brown field, the lines usually wavy or broken into a series of longitudinal dashes (Fig. 3, *right*), and a black gular band which may be so expanded as to involve the entire ventral surface including the undersides of the arms.

Distribution: The coastal regions of San Cristóbal Province and the Distrito Nacional, from the Río Ozama on the east to the vicinity of Sabana Grande de Palenque on the west (Fig. 11); presumed to occur inland, since individuals were seen crossing the road near the city of San Cristóbal.

Description of type: An adult female with the following measurements and counts: snout-vent length 114 mm, tail 275 mm; ventrals in 38 longitudinal and 12 transverse rows; fourth toe subdigital scales 46 and 46 (total 92); femoral pores 18 and 20 (total 38); 44 scales in the fifteenth caudal verticil. Dorsal ground color rich reddish brown in life, with a series of seven dull longitudinal lines, the median line rather obscure, the lateral lines broken into a series of wavy dashes, the lateralmost lines bordering above the black lateral fields, which have a series of tiny yellow dots enclosed within them. Sides of head gray with a creamy subocular patch and some pale irregular blue blotches. Throat fleshy gray. Ventral color dark blue-gray. Hindlimbs heavily spotted with yellow, forelimbs faintly spotted with blue. A dark gray gular band not involving the chest and underside of the arms. Tail reddish brown above, dark gray below.

Variation: See tables. The series of *A. c. procax* is remarkably uniform in both coloration and pattern. The dorsal ground color is always some shade of reddish brown, and there may be a yellowish green wash over the shoulders. The longitudinal lines are conspicuous, although the median line may be reduced or faint. Only in young and subadult individuals are the lines entire, and even in these specimens there is a strong tendency toward wavy fragmentation. The lateral fields are black and the yellow dots included therein are regularly very tiny; in females these included dots are less well differentiated than in the males. The gular band is present, and in large males may be very extensive, including most of the belly. The venter is blue in juveniles and females, and gray to solid black in males.

Comparisons: The reddish brown dorsal coloration and the wavy dorsal lines separate *procax* from all other races. Some specimens of *chrysolaema* were noted in life as reddish brown, but this is not the usual dorsal coloration of the nominate race. Individuals of *chrysolaema* with this coloration are readily differentiated from *procax* on the basis of the very different dorsal patterns of the two subspecies.

In size, *procax* is closest to *chrysolaema,* although *procax* is distinctly the smaller of the two. *Chrysolaema* is typically a subspecies with 12 rows of ventrals, whereas *procax,* although it has individuals with 12 rows, has a modal condition of 10 rows. *Procax* averages fewer (84.8) fourth-toe scales than *chrysolaema* (86.7), the same as *alacris*, and more than *boekeri* (84.6) and *umbratilis* (83.0). In number of femoral pores, *procax* (36.1) averages far lower than *chrysolaema* (43.7), and slightly lower than *boekeri* (36.5), but slightly higher than *umbratilis* (35.6) and *alacris* (33.8); *procax* is one of the races with a low number of femoral pores. In fifteenth verticil scales, *procax* averages less (42.8) than *chrysolaema* (44.4) and *alacris* (44.0), and is about equal to *boekeri* and *umbratilis* (42.7).

Remarks: A. c. procax is presently not known to intergrade either with *boekeri* to the west or the race next to the east along the southern Hispaniolan coast. The easternmost *boekeri* locality (where the population incidentally is almost completely made up of non-patterned individuals) and the westernmost locality of *procax* are separated by only 35 kilometers. As noted in the discussion of *boekeri,* Baní lies about on the dividing line between the xeric Llanos de Azua to the west and more mesic conditions on the east. *Procax* inhabits these eastern more mesic regions, whereas *boekeri* is restricted to the xeric Llanos de Azua.

AMEIVA CHRYSOLAEMA PARVORIS,[1] new subspecies

Holotype: MCZ 77234, an adult male, from 0.9 mi. (1.4 km) E Boca Chica, Distrito Nacional, República Dominicana, one of a series taken 23 August 1963 by Ronald F. Klinikowski, David C. Leber, and Richard Thomas. Original number V649.

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[1] From the Latin *parvum* (small) and *os, oris* (mouth), a translation of Boca Chica, the type locality.

Paratypes: All from the República Dominicana, as follows: MCZ 81011-14, USNM 152571-74, AMNH 92850-55, KU 79872-74, UIMNH 55638-39, RT 789-90, same data as holotype; ASFS V669-79, Boca Chica, eastern edge, Distrito Nacional, 23 August 1963, R. F. Klinikowski, D. C. Leber, R. Thomas.

Associated specimens: República Dominicana, San Pedro de Macorís Prov., 0.5 mi. S San Pedro de Macorís, at lighthouse, 11 (ASFS X8181-91); *La Romana Prov.*, Isla Catalina, western end, 4 (ASFS V554-57).

Diagnosis: A subspecies of *A. chrysolaema* characterized by a combination of large size (males to 137 mm, females to 113 mm snout-vent length), usually 12 transverse rows of ventrals, moderate number of fourth-toe subdigital scales and femoral pores, and high number of scales in the fifteenth tail verticil; dorsal pattern of tan to blackish brown ground color with dull yellow spots which may be either discrete or confluent, giving a reticulate appearance (Fig. 4, *left*), lateral fields present and black, or broken to give a tigroid effect, and a black gular band which may be expanded to involve the chest and the undersides of the arms.

Distribution: Coastal southeastern República Dominicana, from Boca Chica on the east to San Pedro de Macorís on the west, and including Isla Catalina; range as here described apparently discontinuous, and *A. chrysolaema* unknown from the mainland opposite Isla Catalina (Fig. 11).

Description of type: An adult male with the following measurements and counts: snout-vent length 129 mm, tail 282 mm; ventrals in 38 longitudinal and 10 transverse rows; fourth-toe subdigital scales 41 and 42 (total 83); femoral pores 19 and 19 (total 38); 44 scales in the fifteenth tail verticil. Dorsal ground color dull blackish brown, with the entire back from the neck to the sacrum covered with dull yellow spots, not aligned into linear series; lateral fields black, not bordered above or below, and invaded by the brown dorsolateral coloration, the entire sides spotted with yellow dorsally and pale blue ventrally. Throat gray, ventral ground color gray. A black gular band which extends slightly onto the chest and also the underside of the arms. Forelimbs faintly spotted with bluish, hindlimbs spotted with dull yellow. Tail grayish brown dorsally, gray ventrally.

Variation: See tables. The dorsal ground color of *A. c. parvoris* varies from blackish brown (type locality) to tan and brown (San Pedro de Macorís). The spotted condition of the black is typical of most specimens, including small juveniles,

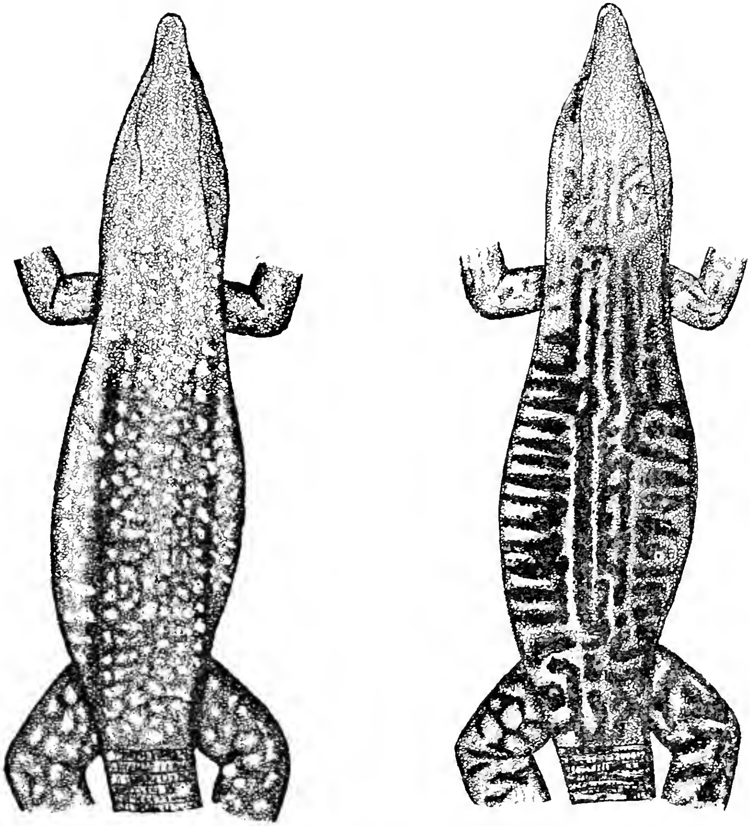

Fig. 4. *Left, Ameiva c. parvoris*, holotype, MCZ 77234, 0.9 mi. E Boca Chica, Dist. Nac., República Dominicana. *Right, Ameiva c. jacta,* holotype, MCZ 75267, Juanillo, La Romana Prov., República Dominicana.

but others show a more lineate pattern somewhat like that described for *procax* — the dorsal lines broken into dashes giving a wavy appearance. The lateral fields may be obscured as in the type, or may be slightly more prominent, with much encroachment of brown to give an irregular and indefinite edge; at the same time the black lateral field pigment may extend up onto the sides of the back, thereby giving a distinctly tigroid appearance to the sides and dorsolateral regions. In some individuals the dorsal spots are confluent, thereby increasing the tigroid effect by transverse dorsal pale markings. The throat is grayish to dull orange and the ventral ground color varies from grayish blue to dull, deep orange.

The small series from Isla Catalina resembles the mainland specimens in dorsal pattern and in extent of the gular band, which in *parvoris* may involve the chest and undersides of the arms. The dorsal dots are conspicuously confluent, the lateral fields are obsolete, and the ventral coloration is pale bluish with an orange tint. The most obvious difference in coloration is that the dorsal surfaces of the hindlimbs are rusty — a feature found in no mainland *parvoris*. The Catalina series is composed of one adult male with a snout-vent length of 126 mm and thus a large lizard, and three females (one of which is a small juvenile), the largest of which has a snout-vent length of 112 mm, again a large lizard. The transverse ventrals are 10 in three specimens and 12 in one. In all other features of scalation the Catalina lot falls within the known range of mainland *parvoris*. Additional specimens from Isla Catalina may well reveal that it is inhabited by still another distinctive race; the strikingly rusty hindlimbs are indicative of at least one major color difference between Isla Catalina specimens and mainland *parvoris*.

Comparisons: No other race of *A. chrysolaema* has the back with irregularly arranged and at times confluent spots, and tigroid sides. This feature alone will distinguish *parvoris* from the previous races. In size, *parvoris* is much smaller than *chrysolaema* and slightly smaller than *procax*, but larger than the remaining subspecies. In fourth toe scales, *parvoris* averages less (83.2) than other races except *umbratilis*, which is comparable (83.0). *Parvoris* averages less (38.2) than *chrysolaema* (43.8) in femoral pores, but exceeds the remaining races, all of which have low femoral pore counts. In fifteenth verticil scales, *parvoris* has the same mean as *boekeri* and *umbratilis* (42.7), less than *chrysolaema* and *alacris* (44.4 and 44.0), and almost the same as *procax* (42.8).

Remarks: A. c. parvoris is not known to intergrade with *procax* on the west nor with the following subspecies to the east. The easternmost locality for *procax* is separated by 35 kilometers from the westernmost *parvoris* record. It is possible that the Río Ozama may divide these two races of *A. chrysolaema*. The area occupied by *parvoris* does not differ in any obvious way from that inhabited by *procax*.

AMEIVA CHRYSOLAEMA JACTA[1] new subspecies

Holotype: MCZ 75267, an adult male, from Juanillo, La Romana Province, República Dominicana, taken 29 March 1963, by Clayton E. Ray and Robert R. Allen.

Paratypes: MCZ 75268-69, same data as holotype.

Diagnosis: A subspecies of *A. chrysolaema* characterized by a combination of large size (males to 134 mm snout-vent length; females unknown), usually 12 transverse rows of ventrals, low number of fourth toe subdigital scales, moderate number of femoral pores, and very low number of scales in the fifteenth caudal verticil; a dorsal pattern of dark brown to black tigroid markings on a grayish tan background (in preservation), the pattern extending in a diluted fashion onto the neck, a bold, checkerboard-patterned tail (Fig. 4, *right*), and a black gular band which extends onto the chest and underside of the arms.

Distribution: Known only from the type locality in extreme eastern República Dominicana (Fig. 11).

Description of type: An adult male with the following measurements and counts: snout-vent length 134 mm, tail 304 mm; ventrals in 38 longitudinal and 12 transverse rows; fourth-toe subdigital scales 41 and 41 (total 82); femoral pores 21 and 22 (total 43); 35 scales in the fifteenth caudal verticil. Dorsum (preserved) tannish gray with a dark brown, almost black pattern consisting of bold vertical tigroid markings on the sides and about five wide, dark, longitudinal lines on the back, the latter much confused and joined by the lateral vertical markings, giving a rather complete and complex dark brown reticulum, which, although present on the neck, is much paler gray. Lateral fields completely absent, no dotting on sides or back whatsoever. Upper surface of forelimbs with obscure grayish lines and blotches, hindlimbs with a dark brown reticulum enclosing large spots which are pale centrally and darker peripherally. Tail with a bold checkerboard pattern of grayish tan, white, and dark brown, this pattern becoming obsolescent and absent on the distal half of the tail. Belly and throat presently dull grayish orange, with some lateral ventral scales with very dark gray blotches, thereby giving the belly somewhat of a faint checkerboard appearance laterally. Black gular band obsolete but indicated, and anterior ten rows of ventrals clouded with dark gray.

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[1] From the Latin for "thrown," an allusion to the far flung distribution of this subspecies.

Variation: See tables. In coloration and pattern the two paratypes are much like the type and require little comment. The major difference is that the paratypes have a bold, black, gular band which involves the chest and the underside of the arms. Neither lizard has any indication of lateral fields, and the sides and back have the tigroid vertical bars and brown to black reticulum, as well as the checkerboard tail, just as described for the type.

Comparisons: A. c. jacta does not need detailed comparison of pattern with any other described subspecies; the boldly and vividly marked back with its light ground color will distinguish *jacta* from the remaining races. *A. c. parvoris* is closest to *jacta* in pattern, but the differences are so striking that the similarity between these two subspecies is not very great.

In size, *jacta* is smaller than *chrysolaema, procax* and *parvoris*, and larger than the remaining forms. All other races have a higher number of fourth-toe scales and fifteenth verticil scales. *Jacta* has a high mean of femoral pores, having less than *chrysolaema*, and more than the balance of the subspecies.

Remarks: No intergradation is known between *jacta* and *parvoris* to the southwest; the easternmost mainland locality for *parvoris* is separated by 145 kilometers from that of *jacta*. We have attempted to secure specimens of *A. chrysolaema* between San Pedro de Macorís and Juanillo at several localities along the coast (La Romana, Boca de Chavón, Boca de Yuma) as well as inland in this eastern region, without success. Typical xeric *chrysolaema* habitats here are occupied by *A. taeniura*. Considering the likeness of *jacta* to the race from Isla Saona, described below, it is probable that this boldly marked type of lizard was at one time (and still is?) abundant locally in extreme eastern Hispaniola. Presently, the hiatus between *jacta* and *parvoris* and the apparent absence of the species in this eastern region suggests strongly that the populations are relict with a disjunct distribution.

AMEIVA CHRYSOLAEMA RICHARDTHOMASI[1] new subspecies

Holotype: MCZ 77235, an adult male, from the environs of Mano Juan, Isla Saona, República Dominicana, taken 19 July 1964 by Richard Thomas. Original number V3018.

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[1] Named for the collector.

Paratypes: ASFS V3019-30, USNM 152575-76, AMNH 92856-58, KU 79875-77, UIMNH 56898-99, RT 935, same data as holotype.

Diagnosis: A subspecies of *A. chrysolaema* characterized by a combination of large size (males to 137 mm, females to 124 mm snout-vent length), usually 10 (but often 12) transverse rows of ventrals, high number of fourth-toe subdigital scales and femoral pores, and moderate number of scales in the fifteenth caudal verticil; dorsal pattern of two phases: (1) back gray-green with

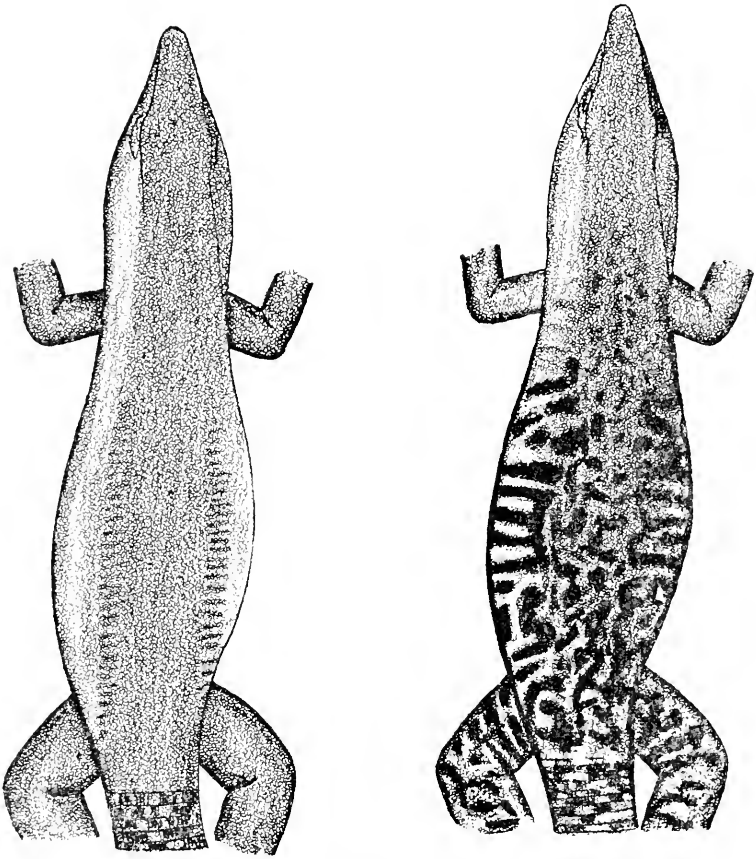

Fig. 5. *Left, Ameiva c. richardthomasi*, holotype, MCZ 77235, environs of Mano Juan, Isla Saona, República Dominicana. *Right, Ameiva c. richardthomasi*, ASFS V3019, environs of Mano Juan, Isla Saona, República Dominicana.

only an indistinct mottling of gray-brown in the area of the lateral fields or (2) back gray-green with heavy black mottling, no lateral fields, and tigroid vertical bars on the sides, the dorsal mottling not extending onto the shoulders and neck (Fig. 5), and without a black gular band.

Distribution: Known only from the type locality, but presumed to occur throughout Isla Saona (Fig. 11).

Description of type: An adult male with the following measurements and counts: snout-vent length 137 mm, tail 146 mm, twice broken and regenerated; ventrals in 37 longitudinal and 12 transverse rows; fourth-toe subdigital scales 45 on left side; femoral pores 22 and 20 (total 42); 38 scales in the fifteenth tail verticil. Dorsal ground color gray-green (Maerz and Paul: pl. 22F1), becoming finely mottled laterally with a series of very faint grayish brown vertical bars in the region of the lateral fields; lower sides putty colored. Throat and venter orange with no black gular band. Fore- and hindlimbs unicolor with back, and patternless. Tail grayish tan without obvious checkerboard pattern above, putty colored below.

Variation: See tables. Sixteen specimens of *richardthomasi* (including the type) are patternless dorsally and have a finely filigreed, grayish brown area in the region of the lateral fields. The tails are gray to tan without a prominent checkerboard pattern as in the patterned lizards. The venters are orange to drab gray, generally slightly more orange in the pectoral region, and grayer posteriorly. Throat and underside of forelimbs are mottled to nearly unicolor orange, sometimes in discrete flecks. The younger specimens have light gray throats. The underside of the hindlimbs and tail is gray to putty colored with some orange on the anterior surface of the femur, and in some specimens on the entire underside of the hindlimb. Two small juveniles (snout-vent length 47 and 51 mm) are in this patternless phase.

Eight specimens (adults and subadults of both sexes) have patterned backs. In this phase, the dorsal ground color is gray-green with a heavy black mottling and strikingly tigroid barred sides. The black dorsal pattern quickly fades at the shoulders and is absent or very suppressed on the neck. The dorsal blotching is much as that described for *jacta*, i.e., a vermiculate or at times longitudinally arranged configuration of black on a lighter ground. In no specimens are the lateral fields apparent and there is no spotting or dotting on the sides. The bellies of these patterned lizards were the same as those of patternless specimens; females of the patterned lizards have the extent and intensity of the orange not so great as do the males. The checkerboard tail is a common feature.

As in *A. c. bockeri*, we have no doubt that the two phases in *richardthomasi* represent two basic patterns, and in no way should be interpreted as an adult phase versus a juvenile and subadult phase. Although the only two juveniles at hand are patternless, there is an intermingling of sizes of both sexes insofar as the two phases are concerned. Just as in *bockeri*, which is represented by a much longer series, there are no intermediates between the two conditions; each lizard is distinctly in one phase or the other .

Comparisons: The patterned phase of *A. c. richardthomasi* requires comparison only with *A. c. jacta* to which race the former is obviously closely allied. The two can easily be differentiated in that *jacta* has a black gular band and the dorsal pattern continues anteriorly onto the neck, whereas *richardthomasi* lacks a gular band and has the pattern faded anteriorly. *Jacta* also is not known to have a patternless phase

The patternless phase of *richardthomasi* requires comparison with patternless *bockeri*. The two are much alike, but *richardthomasi* differs in having the filigreed or mottled lateral field area whereas *bockeri* has an obsolete lateral field and no mottling in this region. Also the dorsal hues of *bockeri* populations are usually not greenish.

In size, *richardthomasi* is smaller than *chrysolaema* and *procax*, equal to *parvoris*, and larger than the remaining races. In having a mean of 87.6 fourth-toe scales, *richardthomasi* averages higher than all previously named races. In femoral pore counts, it is higher than all races except *chrysolaema*. Considering fifteenth caudal verticil scales, *richardthomasi* is exceeded by all forms except *jacta*.

Remarks: The close alliance of *richardthomasi* with *jacta* is obvious. If we assume that extreme eastern Hispaniola is (was) inhabited by a population with heavy dorsal mottling and marbling, this population must also have given rise to the Saonan subspecies. We have no evidence that *jacta* or a related form still occurs on the adjacent Hispaniolan mainland. Certainly *richardthomasi* is an insular derivative of an extreme eastern heavily marked form which was likely similar to *jacta*.

AMEIVA CHRYSOLAEMA LEBERI[1] new subspecies

Holotype: MCZ 77236, an adult male, from 5 km E Pedernales, Pedernales Province, República Dominicana, one of a series taken 25 June 1964 by David C. Leber and Richard Thomas. Original number V2509.

Paratypes: All from the República Dominicana, Pedernales Prov., as follows: ASFS V2510-19, USNM 152577-82, RT 932, KU 79878-81, same data as holotype; MCZ 81015-18, UIMNH 56900-05, Pedernales, 3 July 1964, D. C. Leber, R. Thomas; AMNH 92859-61, 1 km E Pedernales, 25 July 1963, R. F. Klinikowski; AMNH 92862-63, 12 km E Pedernales, 25 June 1964, R. Thomas.

Associated specimens: Haiti, Dépt. de l'Ouest, Tean, nr. Saltrou (not mapped), 4 (MCZ 69389-92); Saltrou, 7 (AMNH 50000-04, 50007-08). *República Dominicana, Pedernales Prov.,* Oviedo, 3 (MCZ 58674-76).

Diagnosis: A subspecies of *A. chrysolaema* characterized by a combination of small size (males to 111 mm, females to 104 mm snout-vent length), 10 transverse rows of ventrals, moderate number of fourth-toe subdigital scales and femoral pores, and low number of scales in the fifteenth caudal verticil; a completely patternless rusty brown dorsum, no lateral fields (Fig. 6, *left*), a deep orange-red belly, and a black gular band which may involve the chest and underside of the arms.

Distribution: To the south of the Massif de la Selle and Sierra de Baoruco, from the vicinity of Saltrou in Haiti, east onto the Península de Barahona, to 12 kilometers southeast of Pedernales (Fig. 11). The record from Oviedo is discussed below.

Description of type: An adult male with the following measurements and counts: snout-vent length 103 mm, tail 233 mm; ventrals in 34 longitudinal and 10 transverse rows; fourth-toe subdigital scales 40 and 42 (total 82); femoral pores 21 and 20 (total 41); 40 scales in fifteenth caudal verticil. Dorsum uniform rusty brown anteriorly, becoming gray-brown posteriorly; sides of head reddish brown. Lateral fields absent. Throat orange, ventral ground color brick red, lower sides (and lateralmost two rows of ventral scales) blue. A black gular band, extending onto the first four or five rows of ventrals and onto the undersides of the arms. Tail gray above, off-white below. Dorsum and top of tail completely unpatterned.

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[1] Named for one of the collectors.

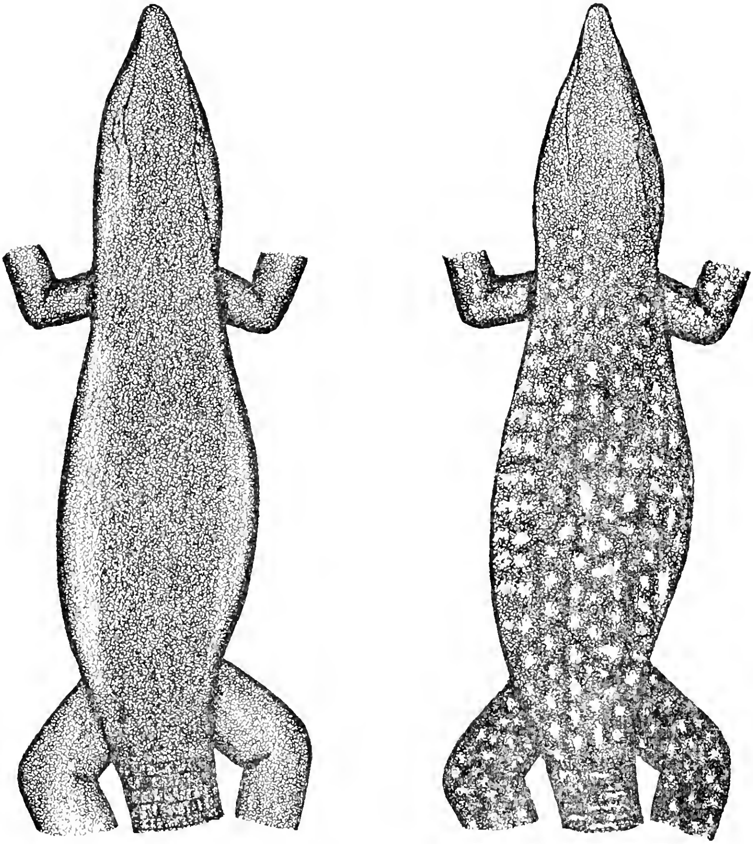

Fig. 6. *Left*, *Ameiva c. leberi*, holotype, MCZ 77236, 5 km E Pedernales, Pedernales Prov., República Dominicana. *Right*, *Ameiva c. ficta*, holotype, MCZ 77237, 13.1 mi. SW Enriquillo, Pedernales Prov., República Dominicana.

Variation: See tables. The dorsal ground color varies from rusty brown to reddish brown, and the ventral ground color from gray with small amounts of red to orange-red, fading posteriorly, to brick red. The gular band is present in all specimens, and in only one male does it not extend onto the chest. The lower sides and lateral two rows of ventrals on each side are blue, or at least have blue flecking, but one small male has the lateral ventrals orange-red like the balance of the venter. The lores and cheeks are unspotted pinkish gray. The tails are gray, unmarked above, and the undersides of the tails are a grayish off-white. There is no obvious sexual dichromatism.

Comparisons: By virtue of its patternless dorsum, *leberi* can easily be differentiated from all races except patternless *bockeri* and patternless *richardthomasi*. The different dorsal hues of *leberi* and *richardthomasi* (rusty brown versus greenish gray) and the presence of a gular band in the former and its absence in the latter, as well as the larger adult size of *richardthomasi*, all make this distinction easy. From patternless *bockeri*, *leberi* differs in smaller adult size, and in lacking any expression of the lateral fields, whereas *bockeri* retains the fields as obsolete grayish longitudinal smudges. The vivid venters of *leberi* are not found in *bockeri*, and the brighter dorsal ground color of *leberi* contrasts strongly with the more drab tones of *bockeri*.

Leberi is the smallest race of *A. chrysolaema*. In number of fourth-toe scales, *leberi* averages lower (85.5) than *richardthomasi* (87.8) and *chrysolaema* (86.7), and is higher than the remaining subspecies. In femoral pores, *leberi* again averages less (41.3) than *chrysolaema* (43.7) and *richardthomasi* (42.6), the same as *jacta*, and more than in the other races. In fifteenth verticil scales, *leberi* is exceeded by all subspecies except *jacta*.

Remarks: A. c. leberi is not known to intergrade with either *chrysolaema* to the north (from whose range it is completely separated by the Massif de la Selle) or with the form to the east on the Península de Barahona. The three specimens from Oviedo noted in "Associated Specimens" above, will be discussed in detail in the treatment of the following subspecies.

AMEIVA CHRYSOLAEMA FICTA[1] new subspecies

Holotype: MCZ 77237, an adult male, from 13.1 mi. (20.8 km) SW Enriquillo, Pedernales Province, República Dominicana, one of a series taken 22 July 1963 by Albert Schwartz and Richard Thomas. Original number X9401.

Paratypes: All from the República Dominicana, Pedernales Province, as follows: ASFS X9402-09, same data as holotype; ASFS X9950, same locality as holotype, 30 July 1963, R. Thomas; ASFS V197-98, same locality as holotype, 4 August 1963, D. C. Leber, R. Thomas.

Associated specimens: República Dominicana, Pedernales Prov., 30 km from Oviedo, road to Pedernales, 1 (MCZ 58673);

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[1] From the Latin for "invented, devised," in allusion to resemblances to *abbotti*.

Oviedo, 15 (MCZ 58677-80, 58682-90, 58692-93); 5 mi. (8 km) NE Oviedo, 11 (ASFS X9957-58, V273-80, RT 752); *Barahona Prov.*, 3 km SW Enriquillo, 1 (ASFS V290); Enriquillo, 2 (MCZ 58777-78).

Diagnosis: A subspecies of *A. chrysolaema* characterized by a combination of moderate size (males to 121 mm, females to 113 mm snout-vent length), 10 transverse rows of ventrals, low number of fourth-toe subdigital scales, moderate number of femoral pores and scales in the fifteenth tail verticil; dorsum tan to brown, spotted with pale blue, lateral fields obsolescent and often replaced by vertical blackish bars or vermiculations (Fig. 6, *right*), belly rust colored, a prominently checkerboarded tail, and a black gular band often extending onto the chest and underside of the arms.

Distribution: The Península de Barahona from (apparently), 30 km NW Oviedo in the west, east to the east coast in the vicinity of Oviedo, and thence north to Enriquillo (Fig. 11); see however *Remarks* below.

Description of type: An adult male with the following measurements and counts: snout-vent length 112 mm, tail 287 mm; ventrals in 36 longitudinal and 10 transverse rows; fourth toe subdigital scales 38 and 39 (total 77); femoral pores 21 and 20 (total 41); 38 scales in the fifteenth caudal verticil. Dorsal ground color brown, with six longitudinal series of more or less discrete pale blue spots, the lateralmost series bordering above the remnants of the lateral fields, below which is another longitudinal series of pale blue spots; lower sides with alternating vertical black and pale blue bars; forelimbs vaguely spotted with small dots, hindlimbs boldly marked with large rusty spots dorsally. Throat grayish orange, belly rust colored; an extensive black gular band which includes the first eight rows of ventrals and extends onto the undersides of the arms. Tail brown above, with blue spots on the first nine verticils dorsally, and additionally somewhat checkerboarded; tail ivory below.

Variation: See tables. The tan to brown dorsum with pale blue discrete spots characterizes *A. c. ficta*. The spots, on occasion, may be greenish anteriorly or tan posteriorly, but in general they are pale blue. The lateral fields are obsolete or almost completely obliterated by vertical black bars alternating with blue bars on the sides. The throat and ventral ground color are grayish orange and rust, with bellies of females slightly paler than those of males. In some individuals the dorsal spots are distinctly lineate in appearance, and in a few the back has a more or less complete finely filigreed appearance, although this is not the norm. The spots themselves vary in size, distribution, and density; they may be much smaller than in the type and much more closely appressed to one another, or the paramedian rows (if rows are discernible) may be fused to form a pair of paramedian pale blue lines. The checkerboard tail with blue spotting on its basal portion is a common feature.

Comparisons: Only one other race thus far discussed, *A. c. parvoris,* has a spotted dorsum, although *A. c. chrysolaema* has a pattern of spots and lines. In neither of these two races are the dorsal spots pale blue, but are rather some shade of yellow. In actuality, the pattern of *chrysolaema*, although dotted, bears little resemblance to that of *ficta;* the pattern of *parvoris* is similar but the coloration and general aspect of the lizards of these two races are quite distinctive. *Parvoris* lacks a conspicuously checkerboarded tail.

Compared to the described races, *ficta* is exceeded in size by all other forms except *leberi*, which is still smaller. In number of fourth-toe scales, *ficta* is exceeded by all races except *jacta*. *Chrysolaema*, *richardthomasi*, *jacta*, and *leberi* exceed *ficta* in mean number of femoral pores, and in this character *ficta* exceeds the balance of the races. *Ficta* averages higher in fifteenth verticil scales than *richardthomasi*, *leberi*, and *jacta*, and lower than the other races.

Remarks: The distribution of *A. c. ficta* encompasses the eastern shore of the Península de Barahona from Enriquillo south to Oviedo, and thence inland toward Pedernales for a distance of 30 kilometers. *Ficta* is not known to intergrade with either *umbratilis* to the north or *leberi* to the west (but see below). The northernmost station for *ficta* is 40 kilometers from the closest record of *umbratilis;* we presume that these two races do not come in contact because of the, at best, narrow and intermittent nature of suitable habitats for *chrysolaema* along the east coast of the Península de Barahona.

There are three specimens (MCZ 58674-76) from Oviedo which are clearly *leberi* and in no way resemble *ficta*. Assuming that these specimens did indeed come from Oviedo, they present a problem. They are the only specimens from the entire eastern coast of the Península de Barahona which are patternless; in our considerable collecting experience in the Oviedo region, we never encountered nor collected any *leberi*-like individuals. There are several possibilities; all of which depend upon the assumed correctness of the locality data for these three specimens: 1) they represent a *leberi*-phase of *ficta;* 2) *leberi* and *ficta* are not both subspecies of *chrysolaema;* 3) *leberi* and *ficta* are both *chrysolaema* derivatives but one has been so long separated from the parent stock that the two forms act as species, with a rather broad (30 km) region of sympatry.

In defense of our arrangement of these two forms as subspecies of *A. chrysolaema,* the following comments are pertinent: 1) There is no incontrovertible evidence that these three lizards are a patternless phase of *ficta.* All of our own Oviedo material is patterned, and there is no indication that there exists a patternless phase of *ficta* (although of course there is this possibility). 2) Since neither *leberi* nor *ficta* intergrades with any other subspecies for reasons of geography, and since both have apparently been long isolated from *chrysolaema* and *umbratilis* to the north, one or both might be logically regarded as a distinct species (if so, then *abbotti* and *ficta* would compose one species, or *leberi* could be so regarded). We feel that *leberi,* despite its complete isolation from *chrysolaema,* is so like patternless *boekeri* and *richardthomasi* that to regard it as a distinct species would be misleading and obscure its clear relationships to the balance of *A. chrysolaema.* A somewhat stronger case may be made for separating *abbotti* and *ficta* at the species level; here again, however, the resemblance of both these spotted forms to *parvoris* for example (as well as the overall similarities of *abbotti-ficta* to the more northern subspecies) tends in our opinion to negate removing these two forms from the species *chrysolaema.* 3) The most appealing interpretation is that one (*leberi*) of the two involved forms has been long separated from its parent stock (*A. c. chrysolaema*), and that once contact between it and another subspecies (*ficta*) has been re-established, the two forms do not intergrade but act as separate species. The present lack of contact between *leberi* and *chrysolaema* and between *ficta* and *umbratilis* suggests that both forms may well have had long independent histories. It is even not improbable that *ficta* has been derived from *abbotti,* rather than the reverse, and thus *abbotti* may have been insularly isolated from *leberi.* Such a combination of situations might argue for species status for both *leberi* and *abbotti-ficta* and we have considered this possibility. On the other hand, such a decision obscures the obvious relationships of these two forms to *A. chrysolaema* (in contrast, for instance, to *A. taeniura* or *A. lineolata*).

Finally, and probably the most important point is that the region between Oviedo and Pedernales still remains little known herpetologically; there is always the possibility that the presumed *leberi* from Oviedo are in actuality from farther west and thus from within the known range of *leberi*. We have tried to adhere in this case to a *via media*, and rather than make assumptions from inadequate data, we consider both *leberi* and *ficta* subspecies of *A. chrysolaema*, although admitting that the situation is not completely clear. Exclusive of these three questionable lizards, the ranges of *ficta* and *leberi* approach very closely; the distance between the nearest localities for the two races is only 15 kilometers.

AMEIVA CHRYSOLAEMA ABBOTTI Noble, 1923

Ameiva abbotti Noble, 1923, Amer. Mus. Novitates, 64:1 (type locality — Isla Beata, República Dominicana).

Diagnosis: A subspecies of *A. chrysolaema* characterized by a combination of small size (males to 117 mm, females to 108 mm snout-vent length), usually 12 transverse rows of ventrals, high number of fourth-toe subdigital scales and femoral pores, and moderate number of scales in the fifteenth verticil; dorsum black with a pattern of isolated spots which are orange or yellowish, becoming blue anteriorly, lateral field absent, the sides spotted with sky-blue spots (Fig. 7, *left*), venter deep brick red to orange posteriorly, and a black gular band which expands to cover the chest and underside of the arms.

Distribution: Known only from Isla Beata, off the tip of Cabo Beata (Fig. 11).

Discussion: *A. c. abbotti* is the most brilliantly colored and striking of the races of *A. chrysolaema*. The combination of black dorsal coloration, orange to yellowish spots middorsally, becoming blue anteriorly, and the vivid blue lateral spots provides a particularly colorful lizard. The forelimbs are black to brown (distally) with blue spots, and the hindlimbs black with proximally blue and distally orange spots. The venter is brick red, grading to orange or pinkish posteriorly, and the lateralmost ventrals are invaded by blue and white spotting. The heads are tan to orange with white or bluish spots on the sides. There is a bold black pectoral band which extends onto the chest and even onto the venter and the undersides of the arms. The underside of the hindlimbs is orange on the thighs and orange

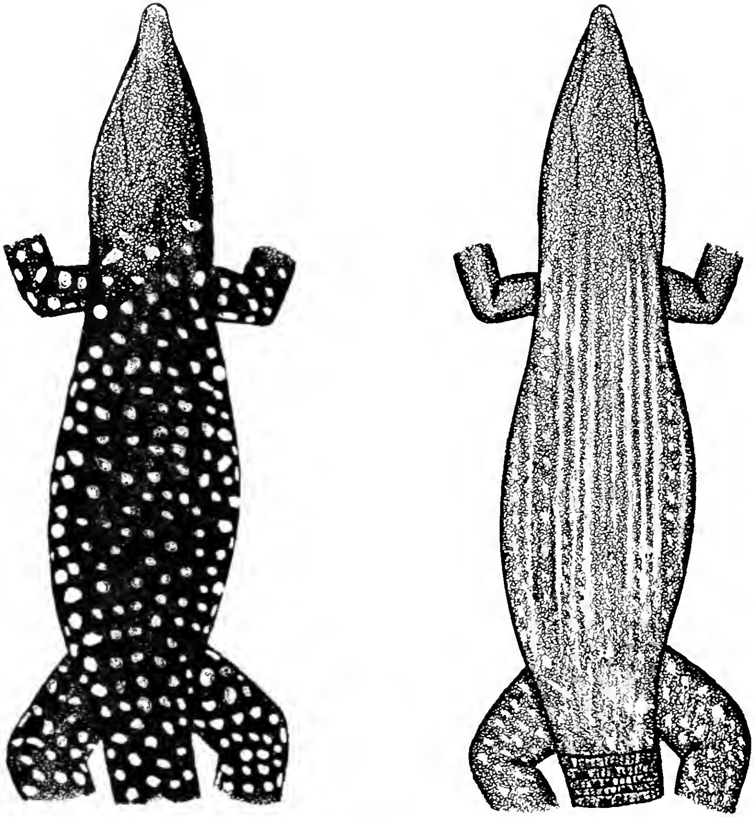

Fig. 7. *Left, Ameiva c. abbotti,* ASFS V2743, Isla Beata, República Dominicana. *Right, Ameiva c. secessa,* holotype, MCZ 77238, Etroits, Ile de la Gonâve, Haiti.

to light tan on the crura. The upperside of the tail is checkerboarded black and white or cream; the underside of the tail is gray to greenish on its proximal half to two-thirds, and uniform light tan to pinkish distally. The dorsal spots are invariably discrete and there is neither a tendency for them to become lineate or to be fused into longitudinal lines. The females are colored and patterned like the males; a juvenile lacks the bright orange ventral color and the black pectoral area.

A. c. abbotti is so very distinctive in its dorsal coloration and pattern that it is hardly necessary to compare it with any other subspecies. Closest, at least in pattern, are *parvoris* and *ficta;* the former, although a dorsally spotted race, is not so gaudy and lacks the discrete spotting so characteristic of *abbotti.* The adjacent race *ficta,* on the mainland, resembles *abbotti* in basic pattern, but differs in having the back brown rather than black, in having the dorsal spots pale blue rather than orange to yellowish, in having the spots at times arranged into lines, and in having the spotting on the back quite variable in density. In contrast, *abbotti* is surprisingly constant in density of dorsal spotting. *Ficta* is primarily a race with 10 rows of ventrals, whereas *abbotti* usually has 12.

Variation: See tables. *A. c. abbotti* has the highest mean (89.6) of fourth-toe scales of any race described to this point, and is approached only by *richardthomasi* (87.8); of all races of *A. chrysolaema, abbotti* has the highest average of femoral pores (43.8), although it is closely approached by *chrysolaema* (43.7). With a mean of 40.4 fifteenth verticil scales, *abbotti* exceeds *ficta, richardthomasi, leberi* and *jacta,* and has less verticil scales than the other races.

The relationships of *abbotti* are obviously with *ficta* on the mainland. Whether the latter occurs on the southern tip of the Peninsula de Barahona is unknown, but it certainly is a more likely candidate there than the drab and patternless *leberi,* if we assume that *abbotti* was derived directly from the adjacent mainland.

Specimens examined: República Dominicana, Isla Beata, 39 (ASFS V2743-69, MCZ 28571-73, 37578-79, 37581-82, 17676-77, 57049, RT 934, UMMZ 83098).

AMEIVA CHRYSOLAEMA SECESSA[1] new subspecies

Holotype: MCZ 77238, an adult male, from Etroits, Ile de la Gonâve, Haiti, taken 17 July 1962 by Elie Cyphale. Original number X2447.

Paratypes: All from Ile de la Gonâve, as follows: ASFS X2440-46, X2448-59, UIMNH 56906-09, USNM 152583-87, AMNH 92864-69, KU 79882-86, same data as holotype; USNM 80377-78, Pointe Ouest, 21 March 1930, L. H. Parish and W. Perrygo; USNM 77062-69, MCZ 25539-48, Pointe à Raquette, August 1927, W. J. Eyerdam; MCZ 80251-78, Pointe à Raquette, summer 1964, G. Whiteman; MCZ 80231-36, Nan Palmiste, 4 km

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[1] From the Latin for "distant, removed."

from Pointe à Raquette, summer 1964, G. Whiteman; MCZ 80237-50, Ti Roche, 0.5 km from Pointe à Raquette, summer 1964, G. Whiteman; USNM 80359-68, 80370-76, UMMZ, 92196, Anse à Galets, 23 March 1930, L. H. Parish and W. Perrygo; MCZ 37568-77, Anse à Galets, 9 April 1934, T. Barbour; USNM 76803, Nan Café, March 1929, A. J. Poole and W. Perrygo.

Associated specimens: Ile de la Gonâve (no other locality), 3 (CM 8133, MCZ 12870-71).

Diagnosis: A subspecies of *A. chrysolaema* characterized by a combination of large size (males to 134 mm, females to 111 mm snout-vent length), usually 12 transverse rows of ventrals, high number of fourth-toe subdigital scales, and moderate number of femoral pores and scales in the fifteenth caudal verticil; dorsum reddish brown with six or seven dull buffy longitudinal lines, grayish brown (rather than black) lateral fields with isolated buffy dots enclosed therein (Fig. 7, *right*), and with the black gular band usually absent, or at least very restricted, seldom involving the anterior ventrals but at times extending onto the underside of the arms.

Distribution: Ile de la Gonâve, Haiti (Fig. 11).

Description of type: An adult male with the following measurements and counts: snout-vent length, 117 mm, tail 134 mm, broken; ventrals in 39 longitudinal and 10 transverse rows; fourth-toe subdigital scales 45 and 45 (total 90); femoral pores 21 and 21 (total 42); 42 scales in the fifteenth caudal verticil. Dorsal ground color reddish brown with seven dull buffy longitudinal lines, the median line somewhat broken and indistinct; head dull tan, neck greenish; sides of head gray with whitish blotches. Lateral fields grayish brown with an enclosed series of buffy dots, more distinct posteriorly than anteriorly, the lateral fields set off above by the lateralmost dorsal lines, and below by a series of bluish spots; lower sides spotted with blue. Throat dirty pinkish gray, gular band absent, belly gray. Forelimbs with scattered pale greenish blue spots, hindlimbs profusely dotted with pale yellow. Tail reddish brown above, grayish blue below, with some blue scales on the sides.

Variation: See tables. The large series of *A. c. secessa* at hand shows little variation in pattern; the entire animal invariably is quite dull, and the lateral fields are never conspicuous. The longitudinal lines do not contrast especially strongly with the dorsal ground color and in some topotypes are very obscure and are seen with some difficulty. In many specimens there are six (rather than seven) dorsal lines, the median line being absent. Invariably the gular band is poorly developed or completely absent; if the band is present, it does not involve the anterior ventrals but may send some pigment onto the underside of the arms. The coloration of the venter varies from gray and bluish gray to dull orange-gray. There is no sexual dichromatism.

Comparisons: A. c. secessa is so dull and drab compared to all other races that no comparison is really necessary. It differs from the spotted races *parvoris*, *ficta*, and *abbotti* in being longitudinally lined, and from the patternless races *boekeri*, *richardthomasi* and *leberi* in having a pattern. It is much duller patterned, and likewise differently patterned, from the other lined races — *chrysolaema*, *umbratilis*, *alacris*, and patterned *boekeri*. From *jacta* and *richardthomasi* (in the patterned phase), *secessa* differs in lacking the lateral tigroid markings and in having a quite different dorsal pattern. Perhaps the most cogent comparison is with *chrysolaema* which occupies all the adjacent mainland about the Golfe de la Gonâve. From *chrysolaema*, *secessa* can at once be differentiated by its much more drab coloration and pattern, and by the lack of dotting in combination with lines on the dorsum. Both *chrysolaema* and *secessa* are typically 12-row lizards.

In fourth toe scales, *secessa* has a higher mean than any other race, being approached most closely by *abbotti* (89.6). In number of femoral pores, *secessa* is exceeded only by *abbotti*, *chrysolaema* and *richardthomasi*; in fifteenth verticil scales, *secessa*, exceeds *ficta*, *richardthomasi*, *leberi* and *jacta*, and is exceeded by the means of the balance of the subspecies.

Remarks: Although *A. c. secessa* has presumably evolved from the adjacent *A. c. chrysolaema*, in dorsal pattern it grossly resembles *alacris* and *procax*, but is quite distinct in several features, notably the obscure lateral fields and the lack of a gular band. It seems likely that the nominate race has carried the pattern evolution — i.e., disintegration of the longitudinal lines into a series of dots — farther than has the isolated *secessa* which has become faded and pale in contrast to its more brightly colored neighbor. Another possible origin of *secessa* is discussed below.

AMEIVA CHRYSOLAEMA DEFENSOR[1] new subspecies

Holotype: MCZ 63379, an adult male, from Môle St. Nicholas, Dépt. du Nord Ouest, Haiti, one of a series taken 24-29 July 1960 by A. S. Rand and J. D. Lazell, Jr.

Paratypes: All from Haiti, Dépt. du Nord Ouest, as follows: MCZ 63368-72, 63374-78, same data as holotype; MCZ 63364-67, Jean Rabel, 26 July 1960, A. S. Rand and J. D. Lazell, Jr.; AMNH 49856-57, Port à l'Ecu, 1 April 1935, W. G. Hassler; USNM 59925, Baie des Moustiques, 3 May 1917, W. L. Abbott; AMNH 49851-55, river just W Port-de-Paix, 2 April 1935, W. G. Hassler; MCZ 58014, river just W Port-de-Paix, 2 August 1935, W. G. Hassler.

Associated specimens: Haiti, Dépt. du Nord Ouest: Bombardopolis, 1 (MCZ 63381); *Dépt. de l'Artibonite,* Gros-Morne, 1 (MCZ 63380).

Diagnosis: A subspecies of *A. c. chrysolaema* characterized by a combination of moderate size (males to 126 mm, females to 106 mm snout-vent length), 10 transverse rows of ventrals, low number of fourth toe subdigital scales and scales in the fifteenth caudal verticil, and moderate number of femoral pores; dorsal pattern a series of six or seven dull longitudinal lines on a tan to brown background, lateral fields dull brown, not especially contrasting with the dorsal ground color and often with the included light spots in the lateral field much reduced or completely absent, a checkerboard tail pattern (Fig. 8, *left*), and no indication of a black gular band, black on the anterior ventrals, or extension of black pigment onto the underside of the arms.

Distribution: The northwest peninsula of Haiti, from Bombardopolis in the south to the vicinity of Port-de-Paix in the northeast, and thence south to Gros-Morne (Fig. 11).

Description of type: An adult male with the following measurements and counts: snout-vent length 118 mm, tail 242 mm, partially regenerated; ventrals in 38 longitudinal and 12 transverse rows; fourth-toe subdigital scales 44 and 44 (total 88), femoral pores 19 and 18 (total 37); 38 scales in the fifteenth verticil. Dorsal ground color (in preservative) dull brown with a series of seven tan longitudinal lines, the median line the least conspicuous, all lines disappearing on the neck. Lateral fields brown, with included tan dots only in their posterior thirds, the anterior

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[1] For the Latin for "defender" in allusion to the English fort at Môle St. Nicholas which guarded the Windward Passage.

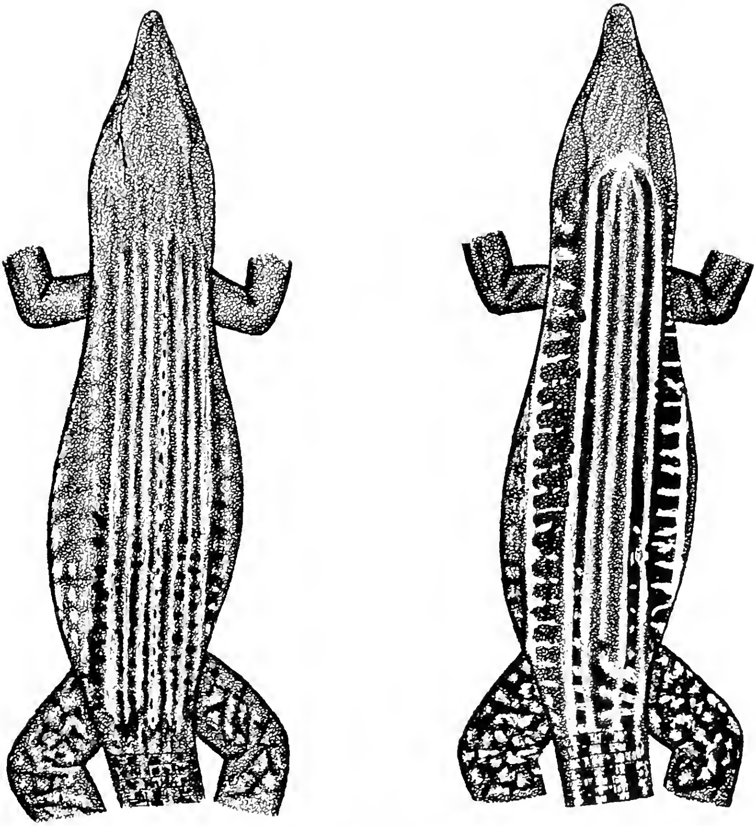

Fig. 8. *Left, Ameiva c. defensor,* holotype, MCZ 63379, Môle St. Nicholas, Dépt. du Nord Ouest, Haiti. *Right, Ameiva c. woodi,* unnumbered specimen from MCZ 37583-92, Ile de la Tortue, Haiti.

two-thirds being without dots. Forelimbs grayish tan, vaguely dotted, hindlimbs brown with large pale spots, leaving almost a reticulum of dark brown surrounding the large pale areas. Ventral ground color (including throat) bluish gray, no black pigment on throat, chest, or undersides of arms. Lower sides with gray and blue markings which are almost tigroid. Tail tan, heavily checkerboarded with dark brown above, blue-gray marked with cream below, and with black and some cream on sides.

Variation: See tables. We are somewhat handicapped in discussing *A. c. defensor* since we have not seen this subspecies in life. Judging from the material at hand, especially the fresh specimens from the Museum of Comparative Zoology (old material in the American Museum from Port-de-Paix and Port à l'Ecu is so discolored that it is completely worthless insofar as coloration is concerned but does still retain some evidences of pattern), *defensor* is typically a dull and drab lizard with dorsal coloration of tan to brown with six or seven longitudinal buffy lines. The lateral fields are brown and have the included dots much reduced (often absent anteriorly) or completely absent. In the latter case the lateral field presents an unbroken brown lateral band. In some specimens, the longitudinal lines have become more obscure than in the type, due to light pigmented areas in the interline regions, and in one extreme case (MCZ 63378 — snout-vent 119, and thus not the largest male) the entire back is marbled with dark and light and the sides are tigroid, the latter a condition noted to a slighter degree in some other individuals. No specimen has any indication of black on the chest or undersides of the arms, and the gular black band is lacking completely. The prominently checkerboarded tail is a constant feature and is plainly discernible even in old and discolored individuals.

Comparisons: A. c. defensor most closely resembles *A. c. secessa* from Ile de la Gonâve. However, the reduced or absent dotting in the lateral fields, smaller size, and the generally somewhat brighter dorsal pattern (although *defensor* is nonetheless a rather drab lizard) will distinguish the two races. *Secessa* usually has 12 rows of ventrals, *defensor* usually has 10. From the patternless races, *defensor* can be distinguished in having a pattern, and from the spotted subspecies by having a dorsal pattern of longitudinal lines. From the other lined races, *defensor* differs in the lack of a black lateral field with included yellow dots, and lack of a black gular band.

In fourth-toe scales, *defensor* (82.4) exceeds only *ficta* (81.9) and *jacta* (79.7); in number of femoral pores, *defensor* (37.2) exceeds only *boekeri* (36.5), *procax* (36.1), *umbratilis* (35.6), and *alacris* (33.8). In fifteenth verticil scales, *defensor* (38.0) exceeds only *leberi* (37.9) and *jacta* (35.7). In counts of fourth-toe scales and fifteenth verticil scales, *defensor* is quite low in the series of subspecies.

Remarks: A. c. defensor is not known to intergrade with any other subspecies; there are two wide hiatuses, however. The closest approximation of records for *defensor* (Gros-Morne) and *chrysolaema* (St. Marc) is 83 kilometers. To the east, there are no specimens available between Port-de-Paix and Cap-Haïtien, a distance of 70 kilometers.

Although *A. c. secessa* is closer geographically to *A. c. chrysolaema,* the former is much more similar to *defensor* than to the nominate race. Such a similarity may be merely convergence and may not reflect direct relationships. It is possible, on the other hand, that *defensor* has reached the northwest peninsula from Gonâve; it seems hardly likely that the reverse is true — i.e., that Gonâve has been colonized from the north — considering the proximity of Gonâve to the adjacent mainland (21 kilometers at its closest point) and its distance from the northwest peninsula (72 kilometers at its closest point).

AMEIVA CHRYSOLAEMA WOODI Cochran, 1923

Ameiva chrysolaemea woodi Cochran, 1923, Occ. Papers Boston Soc. Nat. Hist., 8:181 (type locality — Ile Tortue, Haiti).

Diagnosis: A subspecies of *A. chrysolaema* characterized by a combination of large size (males to 141 mm, females to 126 mm snout-vent length), 10 transverse rows of ventrals, low number of fourth toe subdigital scales, moderate number of femoral pores and scales in the fifteenth verticil; dorsum very dark brown with three to five dull yellowish to buffy stripes or a median dorsal buffy longitudinal band; the stripes may be variously joined and modified to give rather complex dorsal figures which are derived from the simple five lines (Figs. 8, *right;* 9); sides with vertical tigroid markings, and no black gular band or extensions thereof onto the chest and underside of the arms.

Distribution: Ile de la Tortue, Haiti (Fig. 11).

Discussion: The most strikingly patterned and at the same time most variable of the races is *A. c. woodi.* Basically the dorsal pattern is a series of three to five broad, dull yellowish to buffy longitudinal lines on a very dark brown ground. This basic pattern may be modified in that the area between the two paramedian lines may be filled in with a buffy color so that the back has a lateral pair of pale lines and a middorsal pale zone. From this condition, the balance of the back may be filled in with paler, so that the entire back is marked with a single broad pale middorsal zone. In two individuals, the pale lines have

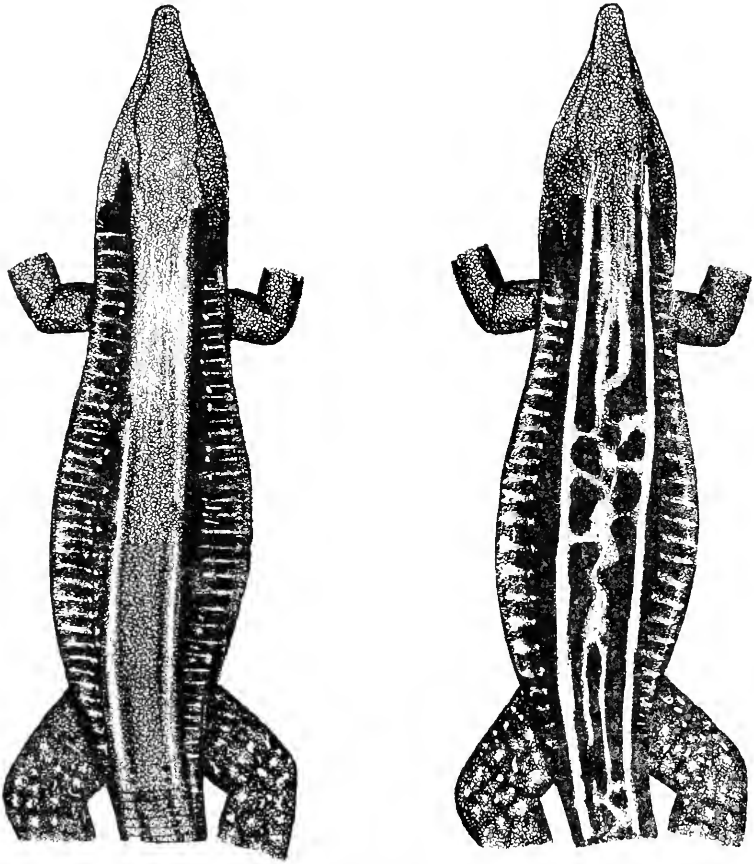

Fig. 9. *Left, Ameiva c. woodi,* ASFS X2270, Palmiste, Ile de la Tortue, Haiti. *Right, Ameiva c. woodi,* ASFS X2267, Palmiste, Ile de la Tortue, Haiti.

grossly fragmented and joined randomly, to form a bizarre, longitudinally reticulate pattern which is quite distinctive. The heads are dull gray-green, with the lores gray. The sides are tan to grayish brown; this lateral color invades the dark brown back to give a series of alternating dark brown and tan vertical tigroid bars, the tan bars often faintly brick colored at their dorsal points. The throats are dirty pale orange, those of the females usually lighter than those of the males (although one female has a brighter orange throat than any other specimen examined in life). The venter is gray, occasionally with a pale orange wash. No specimen has any indication of a black gular band or any black on the chest and undersides of the arms, although there may be some isolated black flecking on the chest. The tails are tan dorsally, with prominent black markings, giving a strong checkerboard effect. The undersides of the tails are gray and often have almost as prominent checkerboarding as the upper surfaces.

Variation: See tables. In pattern, no other race of *A. chrysolaema* is comparable to *woodi;* the three to five longitudinal lines are fewer than in the pattern regularly noted in other subspecies, and the peculiar middorsal broad band, either with or without two dorsolateral lines, and the irregular fragmentation and joining of the lines on a dark brown ground are all features which *woodi* shares with no other race. In lacking a gular band, *woodi* is comparable only to the adjacent *defensor*, and *secessa* and *richardthomasi*. All other forms have the band present. *A. c. woodi* is a remarkably distinct form; it resembles none of the mainland races and is particularly unlike the adjacent mainland *defensor*.

A. c. woodi is a large subspecies, being exceeded only by *chrysolaema* in size, although *procax* is equal in snout-vent length. *Woodi*, in having a low mean (80.5) of fourth-toe scales, exceeds only *jacta* (79.7) in this count. In femoral pore count, *woodi* is exceeded by *abbotti*, *chrysolaema*, *richardthomasi*, and *secessa*, and has a mean femoral pore count equal to those of *jacta* and *leberi*. The moderate fifteenth verticil count (38.8) of *woodi* exceeds only *richardthomasi*, *defensor*, *leberi*, and *jacta*, and is equal to that of *ficta*.

The derivation of *woodi* must certainly be from the adjacent *defensor* of the mainland. The lack of a gular band, and black on the chest and undersides of the arms, and the ten rows of ventrals are features in common between the two races. There the resemblances cease, however, since *woodi* is a boldly and colorfully patterned lizard, whereas *defensor* is dull and drab. *Defensor* likewise does not exhibit any patterns which are reminiscent of those of *woodi*, although the lack of dots in the lateral fields may foreshadow the absence of these fields entirely in *woodi*.

Specimens examined: Haiti, Ile de la Tortue, Palmiste, 10 (ASFS X2267-76); no specific locality on the island, 29 (MCZ 37583-92 + 19 unnumbered specimens).

AMEIVA CHRYSOLAEMA REGULARIS Fischer, 1888

Ameiva regularis Fischer, 1888, Jahrb. Wiss. Anst. Hamburg, 5:26 (type locality, Sans Souci, Haiti; this locality is the palace of the same name near Milot, Dépt. du Nord, Haiti).

Diagnosis: A subspecies of *A. chrysolaema* characterized by a combination of large size (males to 132 mm, females to 128 mm snout-vent length), usually 12 transverse rows of ventrals, very low number of fourth-toe subdigital scales, moderate number of femoral pores, and high number of scales in the fifteenth verticil; dorsal pattern a series of five to seven pale yellow lines on a tan to brown ground color, occasionally with a clear tan middorsal zone, neck greenish and dorsal ground color often suffused with

Fig. 10. *Ameiva c. regularis.* ASFS V-1215, 9 km NW Villa Vásquez, Monte Cristi Prov., República Dominicana.

blackish, lateral fields black with an included row of yellow dots (Fig. 10), and black gular band present or absent, when present seldom invading the chest or extending onto the underside of the arms.

Distribution: North central Hispaniola, from Cap-Haïtien and Grande Rivière du Nord in the west, east to Fort Liberté, Haiti, and thence to Monte Cristi and throughout the Valle de Cibao as far east as the vicinity of Santiago, República Dominicana; also the Siete Hermanos islands (known from Isla Muertos, Torurú, Monte Chico, and Tercero) and Isla Cabras to the north of Monte Cristi (Fig. 11).

Discussion: Cochran (1941: pl. 8, figs. B and D) has illustrated two phases in the dorsal pattern of *A. c. regularis* from Cap-Haïtien, which is near the type locality of the subspecies. Generally, throughout its wide range on the mainland, *regularis* is fairly consistent in dorsal pattern. Specimens from the Valle de Cibao, Monte Cristi, and Pepillo Salcedo, which we have seen in life, were brown dorsally, often suffused with blackish, with a greenish wash on the neck, and had five to seven longitudinal pale yellow lines. At times there is a clear tan middorsal zone resulting from fusion of stripes and filling in of the interspaces with tan. The lateral field is black and prominent with a longitudinal series of yellow dots. The lower sides are dotted with blue-green, and the sides of the belly are bright blue. The ventral ground color varies from grayish to deep dull orange, and the throat from yellowish to gray-orange. The forelimbs are spotted with blue-green, the hindlimbs with yellow. The gular band may be either present or absent; if present, it is not extensive and seldom encroaches upon the chest or extends onto the undersides of the arms.

There are variants of the above basic pattern, such as that shown by Cochran (1941: pl. 8, fig. D), in which there are faint filigreed lines in a middorsal zone. Some specimens show accessory dots between the longitudinal lines, especially posteriorly; in the series from near Villa Vásquez, Monte Cristi Province, two in life clearly showed a secondary dorsal condition, similar to that typical of adult *A. c. chrysolaema,* in which the dorsal lines are supplanted by a series of bright yellow dots overlying the fainter longitudinal lines. In general, specimens from near Cap-Haïtien seem somewhat darker than those from the xeric Valle de Cibao, but in features of pattern they are not remarkably different from those from the Valle de Cibao. Occasional specimens from the western portion of the range of *regularis* have the yellow dots in the lateral fields very tiny, and the field thus appears, grossly, to be immaculate, as is characteristic of some *defensor*.

A series of three adult male lizards from Isla Cabras, off the coast just north of Monte Cristi differs from mainland material in having dark brown lateral fields, and yellow dots on the lower sides. These three specimens also have extensive black gular bands involving the chest and the undersides of the arms. Neither in size nor scalation do there seem to be any differences between these lizards and those from the adjacent mainland. We consider them as *regularis* since in most features of pattern and coloration they are very close to that race.

There are 17 specimens from the Siete Hermanos, a group of seven islets off the mouth of the Río Yaque del Norte. Of these lizards, ten are from Isla Muertos, two from Isla Tercero, two from Isla Torurú, and three from Isla Monte Chico. In coloration, pattern, and scalation they do not differ from mainland specimens, and we regard them as *regularis*.

Variation: See tables. *A. c. regularis* may be differentiated by its lined pattern from the patternless races — *boekeri, leberi, richardthomasi* — and those which have distinct patterns (dots, vermiculations, etc.) — *parvoris, jacta, richardthomasi, ficta, abbotti*. From the lined races, *regularis* differs in lacking a dotted and lined dorsum in combination (*chrysolaema*), in having a dark ground color dorsally and complete and black lateral fields (*defensor, secessa*), in almost always lacking a pattern of a middorsal tan zone and at times having a black gular band (*woodi*), and in having twelve rather than ten rows of ventrals (*boekeri, alacris, procax, umbratilis*). *Regularis* most closely resembles *alacris* and *procax;* compared with *alacris, regularis* reaches a larger size and averages fewer fourth-toe subdigital scales (77.8 versus 84.8). From *procax, regularis* differs in smaller adult size and in often lacking a black gular band, which *procax* regularly possesses. The two subspecies differ in fourth-toe scales, with *regularis* having a lower mean (77.8) than *procax* (84.8).

The north central subspecies is not known to intergrade with either of its neighbors; there are no specimens to the west between Cap Haïtien (*regularis*) and Gros-Morne (*defensor*), a distance of 70 kilometers. The closest approximation of *regularis* (Fort Liberté) and *alacris* (Cerca-la-Source) is 58 kilometers. The intervening mountains almost certainly completely separate these two subspecies.

The distribution of *A. c. regularis* along the northeastern coast of Haiti and thence into the Valle de Cibao in the República Dominicana suggests that this form has evolved along the northern coast and thence has penetrated into the xeric cul-de-sac of the Valle de Cibao. The affinities of *regularis* with *alacris* suggest strongly that the parent stock has been the latter, yet we cannot visualize any means of dispersal of *alacris* to the north Haitian coast; presently at least the Massif du Nord and the Cordillera Central form insurmountable barriers. One route of dispersal suggests itself: the valleys of the Grande Rivière du Nord and the Rivière Bouyaha (the latter a member of the Artibonite system whose upper valleys are occupied by *alacris*) approach each other in the Département du Nord. These valleys and their approximation may have offered a means of ingress for *Ameiva* from the south into the northern Haitian littoral.

Specimens examined: Haiti, Dépt. du Nord, Cap-Haïtien, 14 (USNM 74075-86, MCZ 37593-94); Ti Guinin nr. Cap-Haïtien, (not mapped), 24 (UMMZ 122819 [=12 specimens], MCZ 66527-38); Grande Rivière du Nord, 46 (UMMZ 122820 [=12 specimens], MCZ 63353-63, 66514-26); Fort Liberté, 6 (USNM 76770-75); *República Dominicana, Monte Cristi Prov.*, Laguna de Salodillo, 7 km S Pepillo Salcedo, 1 (ASFS V1430); 4 km E Pepillo Salcedo, 8 (ASFS V1149-55, V1166); Isla Cabras, 3 (ASFS V1372-74); Monte Cristi, 1 (MCZ 58018); 2 km SE Monte Cristi, 5 (ASFS V1210-12, V1284-86); 9 km NW Villa Vásquez, 14 (ASFS V1214-25, RT 811-12); 5 km W Guayubín, 15 (ASFS V1494-508); 7 km N Guayubín, 13 (ASFS V1471-83); *Valverde Prov.*, 9 km N Los Quemados, 1 (ASFS V1766); 7 km E Valverde, 10 (ASFS V2931-40); 2 km E Esperanza, 5 (ASFS V1755-59); *Santiago Prov.*, 7 km W Santiago, 2 (ASFS V2925-26); Santiago and vicinity, 6 (MCZ 58665-66, 58668-71); *Siete Hermanos*, Isla Muertos, 10 (ASFS V1590-95, RT 826, USNM 76733-35); Isla Monte Chico, 3 (USNM 76715-17); Isla Tercero, 2 (USNM 76736-37); Isla Torurú, 2 (ASFS V1573-74).

DISCUSSION

Before proceeding to a discussion of the variation and possible history of *Ameiva chrysolaema* in Hispaniola, we would like to bring out several facts which seem especially worthy of mention.

The distribution of patternless races, or at least races which have some patternless members (*leberi*, *boekeri*, *richardthomasi*),

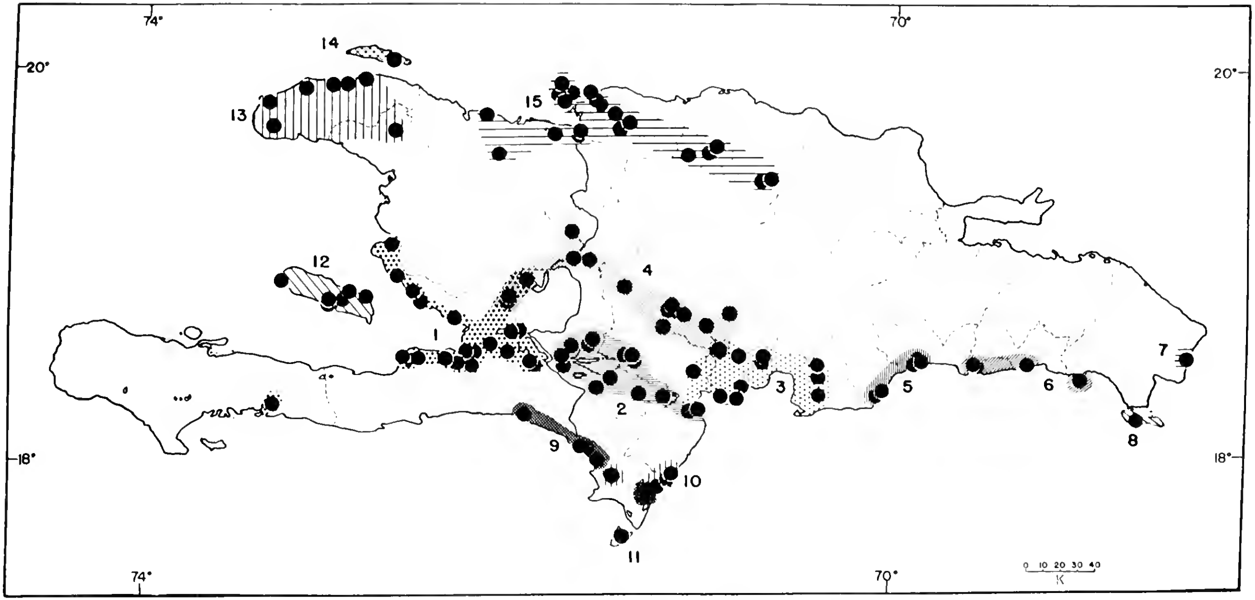

Fig. 11. Hispaniola, showing the known distribution of the races of *Ameiva chrysolaema*, as follows: 1) *chrysolaema*, coarse stippling; 2) *umbratilis*, fine horizontal lines; 3) *boekeri*, open stippling; 4) *alacris*, medium stippling; 5) *procax*, fine vertical lines; 6) *parvoris*, fine diagonal lines; 7) *jacta*, medium horizontal lines; 8) *richardthomasi*, medium diagonal lines; 9) *leberi*, fine crosshatching; 10) *ficta*, medium vertical lines; 11) *abbotti*, fine stippling; 12) *secessa*, open diagonal lines; 13) *defensor*, open vertical lines; 14) *woodi*, coarse crosshatching; 15) *regularis*, open horizontal lines. Overlap of symbols of *chrysolaema*, *boekeri*, and *alacris* indicates area of intergradations between these subspecies. Note disjunct ranges of *chrysolaema* (at Aquin) and *parvoris* (on Isla Catalina). Overlap of symbols for *leberi* and *ficta* at Oviedo does not imply intergradation.

is especially interesting. Of these subspecies, one (*leberi*) is isolated on the south shore of Hispaniola below the La Selle-Baoruco massifs; *leberi* approaches, insofar as known without intergradation, the very different patterned race *ficta* on the Península de Barahona. Another (*boekeri*) has patterned individuals, and is surrounded by three patterned races, of which it intergrades with one (*alacris*), is separated from another (*umbratilis*) by the Río Yaque del Sur, and from the third (*procax*) by a distinct and dramatic change of environment. Finally, *richardthomasi* on Saona has patterned and patternless individuals; this subspecies is related most closely to *jacta*.

Three races are dorsally spotted: *abbotti* and *ficta* on Beata and the Península de Barahona, respectively, and *parvoris* on the southeastern coast of Hispaniola. *Parvoris* is separated from its neighbor to the west, *procax*, by the Río Ozama, and from its eastern neighbor, *jacta*, by a wide gap which is apparently presently uninhabited by *A. chrysolaema*. The occurrence of *parvoris* on Isla Catalina, to the east of the known mainland distribution of that race, is noteworthy.

Of the striped races, *chrysolaema* stands alone in its large size and its style of dorsal patterning, a combination of lines and dots. *Chrysolaema* is known to intergrade with *alacris*, another striped race, in the vicinity of Mirebalais, but no intergrades are known between *chrysolaema* and *umbratilis* in the Cul de Sac-Valle de Neiba. *Umbratilis* resembles the striped phase of *boekeri* to some extent; the two are not known to intergrade. The races *procax*, *alacris*, and *regularis* are all comparably striped; of them, *alacris* and *procax* have 10 rows of ventrals, whereas *regularis* has 12 rows of ventrals. The range of *alacris* is separated from that of *procax* by the intervening and quite different *boekeri*. *Defensor*, by virtue of its pallid coloration and drab pattern, stands alone among the mainland races, but it is approached somewhat by the drab *secessa* from Gonâve; *secessa* has 12 rows of ventrals, *defensor* 10. The Tortue subspecies *woodi* is very distinctive, but logically must have been derived from either *defensor* or *regularis*, the only two races on the north coast.

The Sierra de Neiba and the Montagnes du Trou d'Eau form the northern boundary of the Cul de Sac-Valle de Neiba plain, which is in actuality a fossil strait that once separated Hispaniola into two distinct islands, the north and south islands The south side of the same plain is bounded by the Massif de la Selle and its associated northern ranges (Morne l'Hôpital, Mont des Enfants Perdus) and the Sierra de Baoruco. Considering only this region, one is struck by the amazing diversity of the four races of *A. chrysolaema* associated with it: *chrysolaema* in the northwest, *umbratilis* in the northeast, *ficta* in the southeast and *leberi* in the southwest. Here we are involved with four races whose patterns are radically different — *chrysolaema* dark with longitudinal lines and dots, *umbratilis* pale with lines, *ficta* with large dorsal spots, and *leberi* without pattern.

It has become customary to catalogue, if possible, Hispaniolan reptiles and amphibians into either north or south island species — i.e., depending upon their present and presumed past distribution. Although this is somewhat difficult in the present case, we feel that *A. chrysolaema* is a north island species. Except for the isolated occurrence of *A. c. chrysolaema* at Aquin on the Tiburon Peninsula (based on a single specimen), this southwestern extremity of Hispaniola lacks the species; the otherwise westernmost record is from Père, near Léogâne. The occurrence of the very different race *ficta* on the Península de Barahona (and its relative *abbotti* on Beata), as well as *leberi* to the west along the south coast, indicates that the *A. chrysolaema* stock was long isolated on the southeastern portion of the south island, where *ficta* evolved in isolation from the northern mass of the species. The presence of *leberi* along this south shore is most puzzling, especially since it is geographically closest to *ficta* (see *Remarks* under *A. c. ficta* for additional comments), and since it also resembles *bockeri* far to the northeast. Perhaps *leberi* is the more ancient of the two mainland south island races, and its present rather restricted distribution a mere remnant of a range which was once more extensive, especially to the west toward Jacmel. If such is the case, *leberi* might be regarded as a subspecies derived from (pre)*chrysolaema;* a possible source of colonization from the northern shore of the Tiburon Peninsula might be the Vallée de Trouin, the low pass between the north and south shores of the peninsula. It is of course quite possible that additional collecting in the vicinity of Jacmel or between that city and Saltrou will reveal the presence of *leberi;* it is also possible that *chrysolaema* or *chrysolaema* × *leberi* intergrades may be found in the Vallée de Trouin as well.

On the north island, and including the Cul de Sac-Valle de Neiba, we visualize the old coast inhabited by two races, *chrysolaema* and *umbratilis*, much as today *procax* and *parvoris* occur along the south shore of the eastern República Dominicana. With the closure of the strait, each of these races has expanded into the resulting xeric plain, although to the northwest along the Golfe de la Gonâve, *chrysolaema* still occupies the narrow coastal plain and adjacent xeric foothills much as it may formerly have done farther south. Once across the plain, *chrysolaema* has extended its range inland to some extent (Pétionville), and to the west (Père, Momance). *Umbratilis*, on the other hand, has not been able to penetrate far into the adjacent mountains, although it does reach an elevation of 1000 feet near El Naranjo. The range of *umbratilis* is bounded on the north by the valley of the Río Yaque del Sur.

To the east of the Río Yaque del Sur are a series of four, more or less coastal, races. Of these, *boekeri*, immediately to the north and east of the Yaque, is rather like *umbratilis* in its patterned phase. We consider *boekeri* as a direct derivative of *umbratilis* and restricted to the Llanos de Azua. The next three races — *procax, parvoris, jacta* — show increasingly scattered patterns of distribution to the east, with *jacta* apparently the most isolated. As noted previously, *procax* and *boekeri* approach one another in the vicinity of Baní, precisely in the area of rapid transition from the xeric Llanos de Azua to the more mesic coastal areas to the east. The Río Ozama separates *procax* from *parvoris*, which is known from only two localities on the mainland and from a slightly differentiated population on Isla Catalina. We consider *boekeri, procax*, and *parvoris* as a more or less sequential coastal series still maintaining its integrity in response to environmental and geographical influences.

Jacta, on the other hand, along with *richardthomasi*, represents a very different sort of lizard. We feel that the *jacta-richardthomasi* populations at one time (and perhaps still) occupied most of the extreme eastern end of the island. The presently restricted and scattered distribution and records for not only *jacta* but also *parvoris*, as well as the isolated occurrence of *parvoris* on Catalina, suggest strongly that the range of *A. chrysolaema* in this region is retracting, leaving isolated outliers which may be indicative of former populations. The absence of records of the species between San Pedro de Macorís and Juanillo, as well as only two general localities of *parvoris* on the mainland, add substance to this supposition. The eastern distribution of *Ameiva lineolata* tends also to bear out this contention.

Of the remaining races from the southern part of the north island, only the striped *alacris* is left. *Alacris* is so like *procax* in many features that it is difficult not to associate the two. On the other hand, they are separated presently by *bockeri,* with which race *alacris* intergrades, as it does with *chrysolaema* on the west. It is possible that *alacris* and *procax* were at one time confluent, but that *bockeri* has pushed between them, thereby severing any direct genetic continuity between the two. Another possibility is that *alacris* has been derived from *chrysolaema*, either across the Montagnes de Trou d'Eau or along the valley of the Rivière de l'Artibonite. Continued evidence of intergradation between these two races near Mirebalais lends support to this possibility.

A. c. defensor on the northwestern peninsula has obviously been long isolated from its more southern relatives. Presumably it has been derived from *chrysolaema*. The Gonâve race *secessa* resembles *defensor* in pattern and coloration, and it is possible that Gonâve was colonized from the north (*defensor*) rather than from the adjacent mainland (*chrysolaema*). The latter, however, seems more likely both on the basis of proximity and what is presently known of the origin of the Gonâve herpetofauna.

The relationships of *regularis* seem closest to the *procax-alacris* pair; possibility of origin of *regularis* from *alacris* via the Artibonite system and thence to the Grande Rivière du Nord has already been discussed. Other possibilities are an old origin from *defensor* (although this is not particularly appealing) or an origin from *procax* via the central valley to the east of the Cordillera Central in the República Dominicana. The only evidence against this is that *A. chrysolaema* does not occupy this valley today, although *procax* occurs at its southern end and *regularis* at its northern end near Santiago.

Finally, *A. c. woodi* on Tortue, although closer geographically to *defensor* than to *regularis*, seems closer in some characteristics to *regularis* than to *defensor*. There are, however, tendencies of pattern in *defensor* which herald the extreme peculiarities of *woodi* patterns. On the other hand, occasional *regularis* have dorsal patterns like some *woodi*. It seems more likely that *woodi* is a direct derivative of *defensor*.

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Subspecies	♂	♀
chrysolaema	160	130
woodi	141	126
procax	141	116
richardthomasi	137	124
parvoris	137	113
secessa	135	111
jacta	134	—
regularis	132	128
umbratilis	130	112
boekeri	126	111
alacris	126	109
defensor	126	106
ficta	121	113
abbotti	117	108
leberi	111	104

Table 1. Subspecies of *Ameiva chrysolaema* ranked according to snout-vent length (in mm) of largest male for each race.

Subspecies	N	Mean and extremes	Transverse ventrals (mode)
secessa	50	91.0 (80-99)	12
abbotti	32	89.6 (84-97)	12
richardthomasi	22	87.8 (80-92)	10
chrysolaema	106	86.7 (76-101)	12
leberi	48	85.5 (78-96)	10
alacris	48	84.8 (77-94)	10
procax	51	84.8 (76-98)	10
boekeri	86	84.6 (73-98)	10
parvoris	42	83.2 (76-92)	12
umbratilis	61	83.0 (73-100)	10
defensor	24	82.4 (77-90)	10
ficta	41	81.9 (75-92)	10
woodi	39	80.5 (66-93)	10
jacta	3	79.7 (77-82)	12
regularis	140	77.8 (67-88)	12

Table 2. Subspecies of *Ameiva chrysolaema* ranked according to means of number of fourth-toe subdigital scales; each race is also characterized by the modal number of transverse rows of ventral scales (but see discussions of *umbratilis*, *procax*, and *richardthomasi*). N = number of specimens examined.

Subspecies	Femoral pores Mean and extremes
abbotti	43.8 (35-52)
chrysolaema	43.7 (33-50)
richardthomasi	42.6 (39-47)
secessa	41.5 (36-46)
jacta	41.3 (39-43)
leberi	41.3 (35-45)
woodi	41.3 (36-46)
ficta	40.9 (33-47)
parvoris	38.2 (24-45)
regularis	37.6 (32-44)
defensor	37.2 (30-41)
boekeri	36.5 (31-41)
procax	36.1 (30-43)
umbratilis	35.6 (28-42)
alacris	33.8 (30-39)

Table 3. Subspecies of *Ameiva chrysolaema* ranked according to mean number of femoral pores; N = same as in Table 2.

Subspecies	Scales in 15th caudal verticil Mean and extremes
chrysolaema	44.4 (37-51)
alacris	44.0 (39-49)
regularis	43.1 (30-52)
procax	42.8 (39-48)
boekeri	42.7 (37-48)
umbratilis	42.7 (38-48)
parvoris	42.7 (38-46)
abbotti	40.4 (36-47)
secessa	40.1 (36-44)
ficta	38.8 (36-46)
woodi	38.8 (34-43)
richardthomasi	38.6 (36-41)
defensor	38.0 (34-41)
leberi	37.9 (34-43)
jacta	35.7 (35-36)

Table 4. Subspecies of *Ameiva chrysolaema* ranked according to mean number of scales in fifteenth caudal verticil; N = same as in Table 2.

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No. 11—*A New Attempt to Construct Life Tables for Kent Island Herring Gulls*[1]

By

RAYMOND A. PAYNTER, JR.

INTRODUCTION

An earlier attempt (Paynter, 1949) to construct a life table for the population of Herring Gulls (*Larus argentatus smithsonianus*) on Kent Island, New Brunswick, yielded results which seemed in conflict with the observed status of the colony. The life table indicated that the population was in a steep decline, although the size of the colony was thought to be constant or possibly even producing a population surplus which was contributing to the general increase in Herring Gulls that had been noted in northeastern North America for nearly half a century. To account for the discrepancy between the life table and what was believed to be the actual status of the population, it was suggested that, (1) the 1935 class (erroneously cited as "1936"), which was utilized to construct the postfledging portion of the table, had been banded too short a time (11 years) to yield all potential recoveries, thereby producing a truncated table; (2) that the 1935 year class may have suffered unusually severe postfledging mortality or that the 1947 year class, which provided data for the egg and nestling portion of the table, may also have been unrepresentative, or possibly both situations had prevailed; (3) that there may have been a loss of bands, particularly among older birds, that caused the calculated survival rate and life expectancy to be lowered.

Fifteen years have elapsed since that study. Additional birds from the 1935 class have been recovered and it is now possible to test the hypothesis that older recoveries might be sufficient to raise the calculated life expectancy and survival rates to levels commensurate with the presumed status of the population. Recoveries from bandings in other years at Kent Island have also accumulated, allowing comparisons between several year classes. Finally, there have been published three additional life tables for the species (Paludan, 1951; Hickey, 1952; Olsson, 1958) and these provide valuable comparative data. It is the purpose of this

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[1] Contribution No. 32 from the Bowdoin Scientific Station, Kent Island, Grand Manan, New Brunswick, Canada.

paper to re-examine the dynamics of the Kent Island Herring Gull population in the light of these developments.

MATERIAL AND METHODS

In calculating ages of banded gulls it has been the custom at Kent Island (e.g., Paynter, 1947; 1949) to begin the year on July first, which is about the earliest chicks are large enough to band. To avoid the inclusion of prefledging mortality in the banding recoveries, bands were removed from any chicks dying before fledging and were placed on other young.

In some banding studies it is necessary to make adjustments for bias resulting from the disproportionate recovery of newly fledged birds in the vicinity of their place of birth (see Farner, 1955). This correction is not required of the Kent Island data because the gulls leave the island shortly after they are able to fly and disperse over a wide area (Gross, 1940) where, presumably, they are no more likely to be recovered than older birds.

Banding began at Kent Island in 1934. The terminal date for data used in this study is 30 June 1963. Thus, the oldest potential recovery would be a bird in its twenty-eighth year. To date the oldest record of a gull banded as a fledgling is an individual caught at Kent Island in its twenty-sixth year and released bearing a new band. The oldest record of a bird dying while still wearing its original band is a gull in its twenty-fourth year; the next oldest is a twenty-second year bird. For purposes of this study only young banded in the six year classes from 1934 through 1939 will be considered. The maximum potential age for birds in the most recently banded year class is twenty-three years, which seems close to the maximum age of recovery that may be expected in the Kent Island population (see p. 514). A few birds older than twenty-six almost certainly will be found in future years, but they probably play an insignificant part in the dynamics of this population.

Heeding Hickey's warnings (1952) of clerical and other errors in the banding records kept by the Fish and Wildlife Service, microfilms of all Kent Island banding schedules and recovery records were obtained through the courtesy of Allen J. Duvall. These were carefully compared with the files at Kent Island and all erroneous and questionable data were eliminated. I have no illusions about the complete accuracy of the resulting material, but considering the fact that hundreds of people have been involved in reporting and handling these data during three decades, no further refinements seem possible. It is believed that the quantity of data is sufficient to offset whatever deficiencies in quality remain.

TABLE I

Kent Island Fledglings Banded and Admissible[1] Recoveries

Year	Banded	Recoveries	Per cent
1934	3,646	125	3.43
1935	10,748	352	3.27
1936	6,665	254	3.81
1937	4,652	146	3.14
1938	2,983	77	2.58
1939	3,000	145	4.83
Total	31,694	1,099	3.47

[1] See below for definition of admissible recoveries.

From 1934 through 1939 nearly 32,000 fledgling gulls were banded on Kent Island (Table I). Discrepancies between the yearly totals in Table I and those published previously (Paynter, 1947) result from the re-analysis of the Fish and Wildlife Service records.

These 32,000 bandings have yielded 1,206 recoveries and returns. It is necessary, however, to remove from consideration records in certain categories. Because the Kent Island life table is to be constructed from a mortality series, no records of living birds ("returns") are admissible. As a consequence, those individuals which were trapped in later years at Kent Island and found bearing bands are eliminated, as are those birds which were reported to the Fish and Wildlife Service as having been "captured and released." On the grounds of uncertainty, whether the banded bird was living or dead, Hickey (1952, p. 94) probably would exclude those records reporting "no information," "observed," "found ill," "caught by fisherman," etc. Some of these reports doubtless pertain to gulls not yet dead when their bands were read, but it seems unlikely that many of these records could have been obtained from birds that were not already weakened from illness or injury and soon to die. For this reason I include these records in the mortality series.

Also eliminated from the study are gulls collected in connection with research at Kent Island and those shot elsewhere under gull control permits. Neither of these hazards operated consistently from year to year.

Lack (1954, p. 91) notes that the inclusion of birds which have been recovered by means of shooting (i.e. "normal" shooting — not systematic control) may introduce bias if this category represents a substantial portion of the recovery sample and if juveniles are more easily shot than adults. In certain instances this may be correct, but if a given cohort is hunted with equal intensity throughout its life span, shooting must be considered to be merely another one of the hazards acting upon a population, such as the stress of weather and the toll of predators. The fact that young birds may be more easily shot than older ones does not bias the sample any more than does the fact that adverse weather or predators may claim more young than adults. On the other hand, banded birds which are shot, or for that matter killed through any human agency, probably are more likely to be reported than birds dying of disease or other natural causes. Human activity, therefore, may appear as a disproportionately high cause of death in the sample of recoveries and may also increase the total number of recoveries. But, as long as the human activity causing death operates consistently throughout the life of a cohort, the recoveries need not be excluded from the mortality series used in preparing a life table.

About five per cent of all Kent Island recoveries are of individuals reported as shot; the true rate is probably higher but, because the species is protected by law, is concealed within the reports as "found," "no information," etc. The actual percentage is certainly not nearly so high as in Europe, where the species is unprotected and where about 60 per cent of all reports are of gulls which have been shot (Paludan, 1951; Olsson, 1958). There is no reason to suspect that the distribution by age or year class of recoveries of Kent Island gulls shot but reported in other categories differs from that of birds accurately recorded as shot. Taking the shooting reports at face value, we find considerable variation in the percentage of these recoveries within various age classes, as well as within year classes. For example, in the 1935 cohort, about 6.5 per cent of the gulls were reported as shot; there were no records of birds shot beyond their seventh year and the percentages of reports from the first year through the seventh year are 8.4, 2.9, 6.5, 4.1, 16.0, 0, and 5.2. In contrast, in the 1936 year class, only 3.6 per cent of the records are of birds shot; the oldest was in its twelfth year and the percentages by age classes run 4.8, 3.0, 0, 0, 5.2, 0, 0, 0, 0, 50.0, 0, and 50.0. The distribution of shooting reports illustrated here is similar in all six cohorts. It is of interest that while shooting occurs only in the first half of the maximum potential life span (there are no records beyond the thirteenth year), there is no clear-cut pattern within this period. One might have expected to find shooting relatively more common among immature (and inexperienced) birds.

Birds recovered after having been rebanded are excluded. If Kent Island gulls lose bands, which they doubtless do, and if the loss is a function of the age of the bands rather than a random occurrence throughout the life span of the birds, this may be evident in the life table, provided it is not obscured by other phenomena, as a declining survival rate. The inclusion of rebanded birds in the study, while possibly giving a truer picture of age-specific survival rates, would introduce another source of bias. Unfortunately, there has been an insufficient number of rebandings to allow an analysis of birds in this category.

The Kent Island life tables are begun with the laying of the first egg, which occurs in late May, roughly one-tenth of a year earlier than the July 1 date taken as the start of the year when calculating the ages of banded birds. Because there were no studies of the survival of the eggs and chicks at Kent Island during the period 1934-1939, the records of the 1947 year class (Paynter, 1949) are used, creating composite tables. The mean incubation period is taken at 28 days, or 0.07 years. In 1947 it was found that 28.6 per cent of the eggs failed to hatch; the mean age of the young at fledging was calculated to be 43 days (0.12 years), and 48.5 per cent of the chicks are believed to have failed to fledge, giving a production of 0.92 fledglings per breeding pair.

KENT ISLAND LIFE TABLES

Composite life tables, using the 1947 prefledging data, for the six-year classes from 1934 through 1939, as well as a table for the combined year classes, are presented in Table II. Semi-logarithmic survivorship curves (l_x) are shown in Figures 1 and 2.

The table and graph for the combined six-year classes (Table II; Fig. 2) indicate that about 63 per cent of the eggs laid fail to produce fledged young (see Paynter, 1949, for discussion). Then there is heavy mortality (45 per cent) from the time of fledging until the following July 1, a somewhat lessened rate for the second year of life (35 per cent), and finally a lower average rate for the bulk of the remaining life span (26.8 per cent for the years 3 through 15). This is the expected pattern for most long-lived avian populations. It suggests that young (post-fledging) gulls are less able to cope with the hazards of their environment and that birds surviving the first two years of life have either learned to avoid more of the hazards, or the less adept ones have been eliminated through natural selection. If data for the oldest age groups were more abundant one might find the mortality rate increasing because of the senility. On the other hand, it is unlikely many animals survive this long in nature and that we shall ever have sufficient data from senile individuals to document this phenomenon, if indeed it does occur.

Examined individually, the life tables and survivorship curves (Table II; Fig. 1) show interesting similarities as well as differences, which one expects of natural populations in a variable environment. For example, in four of the six cohorts the mortality rate declined the year following fledging, but in the 1936 and 1938 year classes it rose. The first year postfledging mortality rate for the 1936 cohort was 36.2 per cent, which is unusually low and as a result was slightly below the rate of the second year (39.5 per cent), which was only a little in excess of the average (35 per cent). The same pattern was displayed, in a more exaggerated manner, in the 1938 cohort. The mortality rate in the first year was a comparatively low 37.7 per cent, but in the second year it jumped to 52.1 per cent, the highest observed. Similar yearly fluctuations occur throughout the life tables. Annual variations in the severity of the weather are presumably responsible for many of these swings, but the problem has not been studied.

Next to be considered is the reproductive potentiality of the colony as indicated by the life tables. North American gulls are assumed to breed in their fourth year (year 3-4) or, in other words, three summers after hatching. This may not be an exact assumption for Drost, Focke, and Freytag (1961) found in a German colony of European Herring Gulls (*L. a. argentatus*) that 20 per cent bred in their third year, 25 per cent in their fourth year, and 55 per cent in their fifth year, with the mean breeding age slightly in excess of four years. Paludan (1951), however, concluded that Danish gulls regularly breed in their third year, basing this on a single observation of a bird of this age in a breeding colony. The gull had some dark areas on the tail and on the lesser wing coverts. From this Paludan assumed that fully adult plumage is attained in the third year and that

TABLE II

Composite Life Tables for Kent Island Cohorts 1934-1939, Utilizing 1947 Prefledging Mortality Data of Paynter (1949)

1934 Cohort

x	l_x	d_x	$1{,}000q_x$	e_x
Age in years	No. surviving to start of age interval out of 1,000 eggs laid	No. dying in age interval out of 1,000 eggs laid	Mortality rate per 1,000 alive at start of age interval	Expectation of life remaining to those attaining the age interval (in years)
0.00-0.07	1,000.0	286.0	286.0	.97
0.07-0.19	714.0	346.3	485.0	1.28
0.19-1.10	367.7	182.4	496.1	2.31
1.10-2.10	185.3	44.1	238.0	3.23
2.10-3.10	141.2	26.5	187.7	3.09
3.10-4.10	114.7	20.1	175.2	2.68
4.10-5.10	94.6	38.4	405.9	2.15
5.10-6.10	56.2	23.7	421.7	2.28
6.10-7.10	32.5	11.8	363.1	2.57
7.10-8.10	20.7	8.9	429.9	2.76
8.10-9.10	11.8	0	0	3.47
9.10-10.10	11.8	3.0	254.2	2.47
10.10-11.10	8.8	3.0	340.9	2.14
11.10-12.10	5.8	0	0	1.98
12.10-13.10	5.8	2.9	500.0	.98
13.10-14.10	2.9	2.9	1,000.0	.50
1935 Cohort				
0.00-0.07	1,000.0	286.0	286.0	.94
0.07-0.19	714.0	346.3	485.0	1.23
0.19-1.10	367.7	176.5	480.0	2.21
1.10-2.10	191.2	70.0	366.1	2.92
2.10-3.10	121.2	30.3	250.0	3.33
3.10-4.10	90.9	23.0	253.0	3.27
4.10-5.10	67.9	20.9	307.8	3.21
5.10-6.10	47.0	13.6	289.4	3.41
6.10-7.10	33.4	10.5	314.4	3.60
7.10-8.10	22.9	4.2	183.4	4.02
8.10-9.10	18.7	4.2	224.6	3.81
9.10-10.10	14.5	2.1	144.8	3.76
10.10-11.10	12.4	2.1	169.3	3.32
11.10-12.10	10.3	4.1	398.1	2.90
12.10-13.10	6.2	1.0	161.3	3.50
13.10-14.10	5.2	2.1	403.8	3.08
14.10-15.10	3.1	1.0	322.6	3.84
15.10-16.10	2.1	0	0	4.43
16.10-17.10	2.1	0	0	3.38
17.10-18.10	2.1	1.1	523.8	2.38
18.10-19.10	1.0	0	0	3.50
19.10-20.10	1.0	0	0	2.50
20.10-21.10	1.0	0	0	1.50
21.10-22.10	1.0	1.0	1,000.0	.50

1936 Cohort

x	l_x	d_x	$1{,}000\ q_x$	e_x
0.00-0.07	1,000.0	286.0	286.0	1.04
0.07-0.19	714.0	346.3	485.0	1.38
0.19-1.10	367.7	133.1	362.0	2.50
1.10-2.10	234.6	92.7	395.1	2.75
2.10-3.10	141.9	39.2	276.2	3.23
3.10-4.10	102.7	23.1	224.9	3.27
4.10-5.10	79.6	27.5	345.5	3.07
5.10-6.10	52.1	18.8	360.8	3.42
6.10-7.10	33.3	8.7	261.3	4.08
7.10-8.10	24.6	4.4	178.9	4.35
8.10-9.10	20.2	5.8	287.1	4.19
9.10-10.10	14.4	2.9	201.4	4.68
10.10-11.10	11.5	1.4	121.7	4.74
11.10-12.10	10.1	2.9	287.1	4.33
12.10-13.10	7.2	1.4	199.4	4.87
13.10-14.10	5.8	1.5	258.6	4.93
14.10-15.10	4.3	0	0	5.49
15.10-16.10	4.3	1.4	325.6	4.56
16.10-17.10	2.9	0	0	5.41
17.10-18.10	2.9	0	0	4.41
18.10-19.10	2.9	0	0	3.41
19.10-20.10	2.9	1.5	517.2	2.41
20.10-21.10	1.4	0	0	3.50
21.10-22.10	1.4	0	0	2.50
22.10-23.10	1.4	0	0	1.50
23.10-24.10	1.4	1.4	1,000.0	.50

1937 Cohort

x	l_x	d_x	$1{,}000\ q_x$	e_x
0.00-0.07	1,000.0	286.0	286.0	.85
0.07-0.19	714.0	346.3	485.0	1.10
0.19-1.10	367.7	176.5	480.0	1.96
1.10-2.10	191.2	52.8	276.1	2.45
2.10-3.10	138.4	37.8	273.1	2.19
3.10-4.10	100.6	22.6	224.6	1.83
4.10-5.10	78.0	30.2	387.2	2.24
5.10-6.10	47.8	20.1	420.5	2.34
6.10-7.10	27.7	5.0	180.5	2.68
7.10-8.10	22.7	10.1	445.0	2.16
8.10-9.10	12.6	0	0	2.50
9.10-10.10	12.6	5.0	396.8	1.50
10.10-11.10	7.6	2.5	328.9	1.16
11.10-12.10	5.1	5.1	1,000.0	.49

1938 Cohort

x	l_x	d_x	1,000 q_x	e_x
0.00-0.07	1,000.0	286.0	286.0	.89
0.07-0.19	714.0	346.3	485.0	1.16
0.19-1.10	367.7	138.6	376.9	2.09
1.10-2.10	229.1	119.4	521.2	2.16
2.10-3.10	109.7	33.4	304.5	2.97
3.10-4.10	76.3	14.3	190.0	3.06
4.10-5.10	62.0	9.6	154.8	2.65
5.10-6.10	52.4	19.1	364.5	2.04
6.10-7.10	33.3	9.5	285.3	1.92
7.10-8.10	23.8	9.5	399.2	1.50
8.10-9.10	14.3	4.8	335.7	1.16
9.10-10.10	9.5	9.5	1,000.0	.49

1939 Cohort

x	l_x	d_x	1,000 q_x	e_x
0.00-0.07	1,000.0	286.0	286.0	1.04
0.07-0.19	714.0	346.3	485.0	1.38
0.19-1.10	367.7	182.8	497.1	2.49
1.10-2.10	184.9	71.0	384.0	3.60
2.10-3.10	113.9	32.0	280.9	4.54
3.10-4.10	81.0	10.1	124.7	5.18
4.10-5.10	70.9	12.7	179.1	4.85
5.10-6.10	58.2	7.6	130.6	4.79
6.10-7.10	50.6	7.6	150.2	4.44
7.10-8.10	43.0	7.6	176.7	4.13
8.10-9.10	35.4	2.5	70.6	3.91
9.10-10.10	32.9	7.6	231.0	3.18
10.10-11.10	25.3	5.1	201.6	2.98
11.10-12.10	20.2	7.6	376.2	2.61
12.10-13.10	12.6	0	0	2.88
13.10-14.10	12.6	7.6	603.1	1.88
14.10-15.10	5.0	2.5	500.0	2.98
15.10-16.10	2.5	0	0	4.48
16.10-17.10	2.5	0	0	3.48
17.10-18.10	2.5	0	0	2.48
18.10-19.10	2.5	0	0	1.48
19.10-20.10	2.5	2.5	1,000.0	.48

Combined 1934-1939 Cohorts

x	l_x	d_x	1,000 q_x	e_x
0.00-0.07	1,000.0	286.0	286.0	.95
0.07-0.19	714.0	346.3	485.0	1.25
0.19-1.10	367.7	165.5	450.1	2.26
1.10-2.10	202.2	71.7	354.6	2.82
2.10-3.10	128.5	33.4	260.0	3.27
3.10-4.10	95.1	20.4	214.5	3.30
4.10-5.10	74.7	23.7	317.3	3.07
5.10-6.10	51.0	15.3	300.0	3.26
6.10-7.10	34.7	9.0	259.4	3.56
7.10-8.10	25.7	6.4	249.0	3.63
8.10-9.10	19.3	3.3	171.0	3.67
9.10-10.10	16.0	4.0	250.0	3.33
10.10-11.10	12.0	2.4	200.0	3.27
11.10-12.10	9.6	3.6	375.0	2.95
12.10-13.10	6.0	1.0	166.7	3.43
13.10-14.10	5.0	2.3	460.0	3.02
14.10-15.10	2.7	.7	259.3	4.18
15.10-16.10	2.0	.3	150.0	4.50
16.10-17.10	1.7	0	0	4.23
17.10-18.10	1.7	.3	176.5	3.23
18.10-19.10	1.4	0	0	2.86
19.10-20.10	1.4	.7	121.4	1.86
20.10-21.10	.7	0	0	2.29
21.10-22.10	.7	.4	571.4	1.28
22.10-23.10	.3	0	0	1.33
23.10-24.10	.3	.3	1,000.0	.33

the bird was merely retarded. This appears to be an unnecessarily complicated interpretation. It would seem more logical to conclude that this was a case of an early breeder. Lacking data for the Kent Island gulls, we shall accept the fourth year as the mean breeding age.

In 1947 the average clutch size at Kent Island was nearly 2.5 eggs (Paynter, 1949). Observations (unpublished) in 1948 indicated a somewhat higher mean for first clutches (ca. 2.75) and a lower mean (ca. 2.00) for clutches replacing those lost through predation, but the average for all final clutches was again close to 2.5 eggs.

Taking the life table for the combined years 1934-1939, we find that from an initial cohort of 1,000 eggs 95.1 birds survive to July 1 of the third summer after hatching. It will be recalled that July 1 is the time when banding of the chicks is first practical and that egg-laying begins about one-tenth of a year earlier, in late May. We must, therefore, take into account birds which are alive at the time of laying but which do not survive until July 1. From the life table it is seen that 33.4 birds die during the third year. If the mortality rate is constant throughout the year, one-tenth, or 3.3 birds, die between the time of laying and the first of July. These individuals may then be added to those alive on July 1, giving a total of 98.4 birds which survive to breed for the first time from 1,000 eggs laid four summers earlier.

If the sex ratio is equal, and there is no evidence that it is not, there is an average of 49.2 pairs alive at the start of the first breeding season. At this point these birds have a mean life expectancy of about 3.3 years. If they breed annually, which they probably do for the greater part of their life spans, and lay a yearly average of 2.5 eggs per clutch, the 49.2 pairs are capable of producing 405.9 eggs. This is only 41 per cent of the number required to maintain a stable population.

The only year class with a life table differing materially from the combined 1934-1939 table is the 1939 cohort, with its generally better survival rate among older birds. The calculated number of birds at the start of the first breeding season is 84.2. The mean life expectancy is about 5.2 years. This would allow for a lifetime production of approximately 547 eggs, which again is still far short of the 1,000 eggs needed for a stable population.

If these life tables accurately represent the dynamics of the Kent Island population, it is obvious that the size of the colony should have been rapidly declining in the 1930's and early 1940's, and that the magnitude of the decline would be so great that it would be apparent to field observers. Only constant, large-scale immigration could obscure this phenomenon. Unfortunately, the colony was not accurately censused until 1940 (Crystal, 1941), when approximately 12,000 nests were counted, and the presence of 3,000 more was estimated. Allowing for the inclusion of "play nests" (Goethe, 1937), there must have been a breeding population well in excess of 20,000 birds. During my field work from 1946 through 1948 the colony was densely populated and I estimated it to contain 25,000 to 30,000 individuals (Paynter, 1949). The late Ernest Joy informed me that he had noticed no change in the size of the colony during his tenure as warden from 1935 to 1948. Thus, we must conclude that the Kent Island population was stable, or at least not noticeably unstable, from at least 1935 through 1948. The possibility remains that the colony was failing to reproduce itself and was dependent

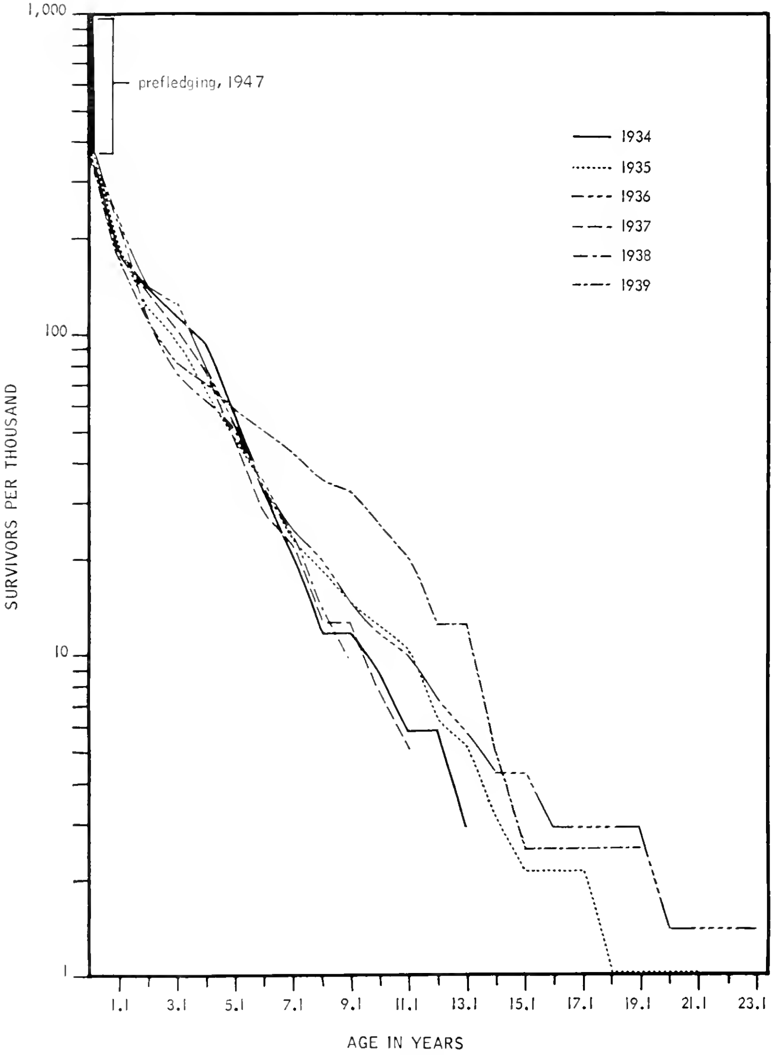

Fig. 1. Survivorship curves for Kent Island cohorts 1934-39.

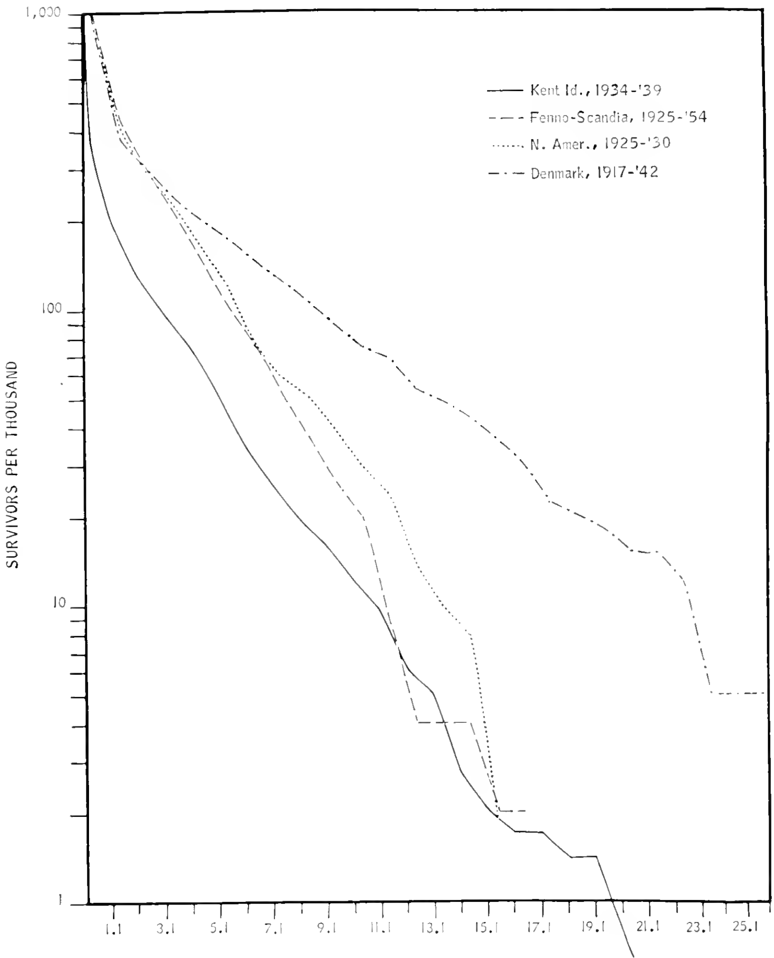

FIG. 2. Survivorship curves for four populations.

on immigrants to maintain a constant size, but this seems improbable. The Herring Gull has been increasing along the eastern seaboard, as well as in Europe, since the turn of the century. It would appear unlikely that the Kent Island colony was not contributing to this general increase. A more reasonable conclusion is that the six life tables are deficient. Before speculating on the possible reasons for this, life tables for other populations of the species will be examined.

OTHER LIFE TABLES

Hickey (1952) has considered the first three life tables prepared for North American Herring Gulls (viz., Marshall, 1947; Paynter, 1947, 1949), commenting on their errors and discrepancies; they need not be reconsidered here. Then using recoveries of gulls banded at various colonies in North America from 1925 through 1930, Hickey constructed an abridged life table for a

TABLE III

Life Table for Theoretical Population of North American Gulls Banded 1925-1930 (504 Recoveries) (after Hickey, 1952)

x	l_x	d_x	1,000 q_x	e_x
0-1	1,000.0	599.2	599.2	2.00
1-2	400.8	117.1	292.1	3.25
2-3	283.7	59.5	209.7	3.39
3-4	224.2	61.5	274.3	3.15
4-5	162.7	41.7	256.2	3.16
5-6	121.0	45.6	376.8	3.08
6-7	75.4	16.1	213.5	3.63
7-8	59.3	7.9	133.2	3.48
8-9	51.4	11.9	231.5	2.95
9-10	39.5	9.9	250.6	2.69
10-11	29.6	5.9	199.3	2.42
11-12	23.7	9.9	417.7	1.90
12-13	13.8	4.0	289.8	1.91
13-14	9.8	2.0	204.1	1.48
14-15	7.8	5.9	756.4	.73
15-16	1.9	1.9	1,000.0	.47

theoretical population of 504 birds, beginning the table with reports received subsequent to 31 August of the year in which the gulls were hatched. No reports were available for gulls older than their sixteenth year. Although the table is probably foreshortened, recoveries beyond the sixteenth year are so infrequent that the resulting table is doubtless close to what would have been found if it had not been terminated until all potential recoveries had been obtained. Adjustments were made for yearly variations in the number of birds banded and for the fact that some birds had not been banded sufficiently long to yield recoveries in the year 15-16 (see Hickey, 1952, p. 11). This life table, recalculated to form a cohort of 1,000, is presented in Table III, and the survivorship curve is plotted in Figure 2.

The first year mortality rate is about 60 per cent, in contrast to an average of 45 per cent at Kent Island from the time of fledging in August to the following June 30, and the second year mortality is 29 per cent, compared to the Kent Island figure of 35.5 per cent. The mean annual mortality rate for the next ten years is 25.6 per cent, which is almost exactly that at Kent Island (Table IV).

Because this table is begun in September, neglecting the egg, nestling, and earliest postfledging mortality, a different technique from that used with the Kent Island data must be employed to assess the reproductive potential of the population.

TABLE IV

Mean Mortality Rates

Population	Age		
	0-1	1-2	2-12
Kent Id., 1934-'39	45.0[1]	35.5	26.0
North Amer. (Hickey, 1952)	59.9[2]	29.2	25.6
Denmark (Paludan, 1951)	62.3[2]	21.7	15.6
Fenno-Scandia (Olsson, 1958)	56.8[3]	31.9	33.8

[1] First interval 0.9 year, i.e. fledging to 30 June following year; 1 July to 30 June thereafter.

[2] Year begins 1 September.

[3] Year begins 1 August.

This is done by totaling the l_x column (survivors) from the year 3-4 (first breeding year) to the end of the table, dividing the total by two to give the number of pairs of breeding birds, and, finally, dividing the initial cohort (1,000) by the number of pairs of breeding birds (see Hickey, 1952, pp. 94-95). The result is the average number of young per pair of adults which need be raised to the first of September of the year of hatching in order to maintain a stable population. Applying this to Hickey's table, we find that an average of 2.44 young must be fledged and survive to September 1. This is only slightly below the mean clutch size found at Kent Island (2.5) and, therefore, allows almost no egg or chick mortality. Even if the mean clutch is assumed to be three, which is the maximum number of eggs laid by Herring Gulls, except for an exceedingly rare clutch of four (about 0.6 per cent of all clutches [Paludan, 1951, p. 49]), this would also allow for but 19 per cent mortality between the laying of the first egg and September 1. Such a mortality rate seems much too low in the light of observations at Kent Island, where more than 60 per cent of the eggs failed to yield fledged young. This life table cannot, therefore, be accepted.

The first life table for a European population of Herring Gulls is that constructed by Paludan (1951) for 966 recoveries, including those shot (ca. 60 per cent), from 11,689 birds banded in Denmark from 1917 through 1942 (Table V). The oldest recovery is that of an individual in its twenty-sixth year; the oldest potential recovery at the time the table was compiled would have been a thirty-fourth year bird. Adjustments, similar to those of Hickey (1952), were made to compensate for the fact that only 8 of the 26 year classes had been banded sufficiently long to yield recoveries in the twenty-sixth year. The mean recovery rate for these eight cohorts was 8.54 per cent, versus only 3.47 per cent for the six cohorts at Kent Island. The marked difference in recoveries is doubtless due to the frequency with which Danish gulls are shot, which enhances the chances that a banded bird will be reported, and also probably due to a better retention of bands, which will be considered subsequently. From this table (Table V), which starts on September 1 following hatching, it is seen that the first year mortality is 62.3 per cent, closely approximating Hickey's finding in North America. The second year mortality drops to 21.7 per cent, which is considerably lower than that in Hickey's table (29.2 per cent) or the Kent Island table (35.5 per cent). The mean annual mortality for the next ten years is only 15.6 per cent, in contrast to the North American

TABLE V

Life Table for Danish Gulls Banded 1917-1942 (966 Recoveries) (Paludan, 1951)

x	l_x	d_x	$1{,}000\ q_x$	e_x
0-1	1,000	623	623	2.72
1-2	377	82	217	5.39
2-3	295	56	190	5.75
3-4	239	37	155	5.98
4-5	202	28	129	5.98
5-6	174	30	172	5.83
6-7	144	18	125	5.95
7-8	126	21	167	5.73
8-9	105	17	162	5.79
9-10	88	14	159	5.83
10-11	74	6	81	5.84
11-12	68	15	221	5.35
12-13	53	4	75	5.68
13-14	49	6	122	5.12
14-15	43	7	163	4.72
15-16	36	6	167	4.56
16-17	30	8	267	4.42
17-18	22	2	91	4.96
18-19	20	2	100	4.37
19-20	18	3	167	3.81
20-21	15	0	0	3.37
21-22	15	3	200	2.37
22-23	12	7	583	1.83
23-24	5	0	0	2.50
24-25	5	0	0	1.50
25-26	5	5	1,000	0.50

and Kent Island rates of about 26 per cent (Table IV). This low rate gives a survivorship curve (Fig. 2) which is strikingly different, after the second year, from those of the Kent Island and North American populations.

Applying the same methods for determining the required productivity of this population as were used with Hickey's data, it is found that to maintain a constant population it is necessary for a pair of gulls to raise 1.3 young to September first following hatching. While this would necessitate about 40 per cent greater productivity than recorded (Paynter, 1949) at Kent Island (0.92 young per pair raised to fledging in early August), it may be a reasonable expectation. On the other hand, the prefledging mortality in Paludan's colony was considerably higher than that at Kent Island. In the Danish colony in 1943 there was about a 10 per cent loss of eggs (vs. 28.6 per cent at Kent Island) and an 80 per cent loss of chicks (vs. 48.5 per cent at Kent Island). With an average clutch of three eggs this heavy mortality would result in a net production of about 0.5 fledgling for each pair of adults or, in other words, only a maximum of 39 per cent of the required productivity as calculated from the life table.

Paludan believed that fledgling production nearly as low as that observed in the Danish population would be sufficient to maintain the population if certain deficiencies in the life table were corrected. He reasoned that the number of birds which breed for the first time should equal the number that die during that year. From the life table he found the mean annual mortality from the second year onward to be about 15 per cent. This would mean that in a population of 1,000 birds, 150 would die during the year and 150 should begin to breed for the first time, if the population is to remain stable. Using the life table figure of 62.3 per cent mortality for the first year and 15 per cent mean annual mortality thereafter, he calculated a production of approximately 600 fledglings per 1,000 adults (1.2 per pair) would be necessary to yield about 150 birds two and a half years later, when he thought breeding began. This would require more than twice as many survivors as he had observed (0.54 per pair). However, Paludan reasoned that the observed first year mortality rate was higher than it should be owing to bias in favor of recoveries near the breeding colonies; a reduction in the first year mortality would increase the number of birds surviving to breeding age and, hence, reduce the required production of fledglings per pair. Also, he believed the prefledging mortality that he had recorded was in excess of that which is normal in Denmark. He concluded that the yearly production of between 0.5 and 1 fledgling per pair of adults would be sufficient to maintain the population, and even allow for the general increase that had been noted throughout Europe.

One significant probable error is the assumption that the entire population begins to breed in the third year. As we have seen above, a few gulls (20 per cent) do breed this early, but the average age is somewhat in excess of the fourth year. When Paludan's statistics are adjusted for this later breeding age, it is found that a pair of gulls would have to produce roughly 1.4 fledglings, rather than 1.2 fledglings.

TABLE VI

Life Table for Danish Gulls, Utilizing Kent Island Prefledging Data and Assuming First Year Recoveries to be Half of Those Actually Recorded

(see p. 508 for explanation)

x	l_x	d_x	$1{,}000\ q_x$	e_x
0-0.07	1,000.0	286.0	286.0	1.43
0.07-0.19	714.0	346.3	485.0	1.92
0.19-1.10	367.7	166.6	453.0	3.56
1.10-2.10	201.1	43.8	217.8	5.37
2.10-3.10	157.3	30.0	190.7	5.73
3.10-4.10	127.3	19.9	156.3	5.96
4.10-5.10	107.4	14.9	138.7	5.97
5.10-6.10	92.5	16.0	173.0	5.85
6.10-7.10	76.5	9.6	125.3	5.97
7.10-8.10	66.9	11.2	167.4	5.75
8.10-9.10	55.7	9.1	163.4	5.81
9.10-10.10	46.6	7.5	160.9	5.85
10.10-11.10	39.1	3.2	81.8	5.88
11.10-12.10	35.9	7.5	208.9	5.36
12.10-13.10	28.4	2.2	77.5	5.64
13.10-14.10	26.2	3.2	122.1	5.07
14.10-15.10	23.0	3.8	165.2	4.71
15.10-16.10	19.2	3.2	166.7	4.54
16.10-17.10	16.0	4.3	268.7	4.35
17.10-18.10	11.7	1.1	94.0	4.77
18.10-19.10	10.6	1.1	103.8	4.22
19.10-20.10	9.5	1.6	168.4	3.65
20.10-21.10	7.9	0	0	3.29
21.10-22.10	7.9	1.6	202.5	2.29
22.10-23.10	6.3	3.7	587.3	1.73
23.10-24.10	2.6	0	0	2.50
24.10-25.10	2.6	0	0	1.50
25.10-26.10	2.6	2.6	1,000.0	.50

If normal fledgling production in the Danish population is assumed to be one per pair of adults, which is the maximum suggested by Paludan, it is necessary for the first year mortality to drop from the observed rate of 62.3 per cent to approximately 52 per cent, in order to replace the 15 per cent loss of breeding birds. This requirement seems reasonable if, as believed by Paludan, there was a disproportionately high recovery of first-year birds in the sample.

It is instructive to note (Table VI) that if the production of fledglings is assumed to be the same as at Kent Island (0.92 young per pair of adults) and if the recovery of first year gulls is halved, the first year mortality rate would be 45.3 per cent, which is almost exactly that found at Kent Island.[1] At sexual maturity there then would be nearly 64 pairs of birds, with a life expectancy of almost six years. If these birds laid an average of 2.5 eggs per clutch, there would be produced about 950 eggs, or nearly sufficient production to maintain the population. If there were three eggs per clutch there would be a net production of about 1,140 eggs, adequate productivity to permit about a five per cent annual increase in fledged birds.

From these calculations one is tempted to conclude that Paludan's first-year recoveries were twice as abundant as they would have been had the birds dispersed as widely as they do in succeeding years and that Paludan was correct in suggesting that breeding pairs need produce only about one fledged chick per year. However, there are certain peculiarities in the recovery data that require examination.

Paludan (1951, Table 29, pp. 108-109) presents a convenient tally of the annual recoveries for the year classes from 1917 through 1942. These records, in contrast to the Kent Island data, show extremely wide annual variations. For example, in the first year after banding the percentage of the total banded birds recovered ranged from 1.0 per cent in 1939 to 26.7 per cent in 1929, and in the second year the range was from 0 in five year classes to 4.0 per cent in 1937. Doubtless some of these great fluctuations are caused by sampling vagaries owing to the small number of birds banded each year and also to wide variations even within these small numbers (15 to 1,291 bandings per year). Nevertheless, there would seem to be some fluctuations which cannot be dismissed as sampling errors. These are well illustrated

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[1] For these calculations it is necessary to assume that the Danish records begin on 1 July and that the first year recoveries are made in nine-tenths of a year, and thus are comparable with the Kent Island data.

by the second year recoveries for the year classes of 1935, 1940, 1941, and 1942, years in which the number of birds banded did not differ greatly. The number of gulls banded in these years was 765, 811, 861, and 710, respectively, and the number of second year recoveries, in the same order, were 0, 11, 1, and 1. Expressed differently, the recovery rates were 0, 1.36, 0.12, and 0.14 per cent.

We need not know the reasons for these fluctuations to appreciate what profound effects they have on a demographic study. The life table constructed by Paludan shows a mortality rate in the second year of nearly 22 per cent, a rate, as has been pointed out, considerably lower than that recorded for any other population. This rate was obtained from data which indicate that about 0.77 per cent of all Danish recoveries were made in the second year. This is the average for all 26 year classes. If, however, we eliminate the year classes for which there were no recoveries during the second year the average rises to 0.96 per cent. Using this figure in the life table would increase the second year mortality rate to 27.6 per cent, and if we employ the figure of 1.36 per cent, which is the percentage of second year recoveries in 1940, the mortality rate rises to nearly 35.8 per cent, which is almost exactly that of the Kent Island population. Concomitant with these increases in the second year mortality rate are decreases in that of the first year, so that in the early intervals the Danish life table becomes quite similar to that of Kent Island.

These calculations should suffice to illustrate that the Danish life table is based on small and highly variable samples, and that even seemingly minor changes in the data may have large-scale effects. This should also warn against assuming that Paludan's life table is more nearly correct than others merely because it "balances" when certain data are borrowed from other populations.

The second life table for European gulls is that prepared by Olsson (1958), for 1,222 recoveries, including those shot (60 per cent), from about 12,700 birds banded in Sweden, Norway, and Finland (=Fenno-Scandia) from the mid-1920's to the mid-1950's (Table VII). The average rate of recovery was about 9.5 per cent, which is nearly three times that at Kent Island and about ten per cent higher than that in Denmark. The table starts on August 1 following hatching. The oldest recovery is a gull in its 17th year; the oldest potential recovery at the time the study ended would be an individual in its 29th year. The raw data have been adjusted to compensate for the fact that some year classes had not been banded long enough to yield all their potential recoveries. It may be seen (Table IV) that the first year mortality of 56.8 per cent is somewhat lower than that found in Hickey's North American and Paludan's Danish populations, and that the second year rate is slightly higher than that of the North American gulls, and considerably higher than that of the Danish birds, but still not so great as that of the Kent Island population. For the next ten years the mean annual mortality is 33.8 per cent, which is more than twice the rate recorded by Paludan and moderately higher than that of the American and Kent Island populations.

Olsson had no records of the fledgling production in the Fenno-Scandian colonies and did not, therefore, attempt to test the accuracy of his life table against such data. Using the method devised by Hickey, it is found that 2.86 fledglings must be raised to

TABLE VII

Life Table for Fenno-Scandian Gulls Banded 1925-1935 (1,122 Recoveries) (Olsson, 1958)

x	l_x	d_x	$1{,}000\, q_x$	e_x
0-1	1,000	568	568	1.93
1-2	432	138	319	2.80
2-3	294	81	276	2.88
3-4	213	66	310	2.79
4-5	147	45	306	2.81
5-6	102	24	235	2.83
6-7	78	26	333	2.55
7-8	52	15	289	2.58
8-9	37	11	297	2.42
9-10	26	6	231	2.23
10-11	20	11	550	1.75
11-12	9	5	556	2.28
12-13	4	0	0	3.50
13-14	4	0	0	2.50
14-15	4	2	500	1.50
15-16	2	0	0	1.50
16-17	2	2	1,000	0.50

August 1 by each pair of breeding gulls if the population is to remain static. Even with a mean clutch of three eggs, such a high rate of nesting success appears improbable and it must be concluded that the Fenno-Scandian life table is also inaccurate.

POSSIBLE ERRORS IN THE KENT ISLAND TABLES

From the fact that the Kent Island colony was observed to have maintained its size from at least 1935 to 1948 (see p. 501) it seems reasonable to conclude that the population was either relatively stable during the 1930's and 1940's or, even more likely, that it was increasing and its surplus overflowed the colony and added to the expanding North American population. The life tables, however, indicate that the population should have been decreasing at a catastrophic rate. If we assume that the life tables are deficient, we must look for a source, or sources, of error within the data used in constructing the tables.

There are three kinds of error which might distort the life tables, causing them to indicate that the population was rapidly declining. First, banding recoveries may have been accumulated for too short a period (23 through 28 years), thereby failing to cover the full life spans of the six cohorts studied. Second, the 1947 egg and prefledging mortality rates, which were used in constructing the initial intervals of all six tables, may have been uncharacteristically high. Third, bands may have been recovered more readily in the early postfledging years than later in the life spans, causing an apparent increase in the mortality rates for the early intervals of the tables.

The first hypothesis, i.e. that a study allowing for recoveries for a maximum period of between 23 and 28 years does not cover the full life span of the Herring Gull, is correct, but probably only to a small and insignificant degree. For example, a Kent Island gull has been found alive in its twenty-sixth year, and a bird banded as an adult was recovered 24 years later meaning it was a minimum of twenty-seven years old when it died. There are also records of captive Herring Gulls which have lived nearly fifty years (Gross, 1940); it is conceivable that some wild individuals may attain an equally advanced age. Nevertheless, it seems that very few gulls live beyond their twenty-third year, which is the oldest potential recovery within the youngest cohort studied at Kent Island, and those birds that do live longer doubtless have little influence on the reproductive rate of the population because of their relatively insignificant numbers and possibly (unproven) because of sterility brought about by senility.

Support for the argument that the life tables adequately cover the life spans of the gulls may be found in the recovery data. Of the 954 recoveries from the five oldest cohorts, with a maximum potential age ranging from 24 to 28 years, only one individual (0.16 per cent) reached the age of 24, none exceeded that, and but three lived more than 18 years. Expressed differently, less than one-fifth of one per cent of the recoveries were of birds older than 18 years. In Paludan's Danish study (1951) there were eight cohorts with a maximum potential age between 26 and 34 years. Of the 236 recoveries from these cohorts there was just one bird in its twenty-sixth year and the recovery rate between the eighteenth and twenty-sixth year was only 0.8 per cent of the total sample. The maximum potential age of birds in Olsson's (1958) Fenno-Scandian population was twenty-nine years, but the oldest recovery was a single seventeenth-year individual.

There is, of course, the possibility that a loss of bands could account for the failure to recover gulls even older than those now known. But it is believed that while the frequency of recoveries may be reduced because of band loss, there is little likelihood that the maximum span of life is significantly greater than that which has been recorded. We must, therefore, seek another explanation for the failure of the life tables to document the population dynamics of the Kent Island colony.

The second hypothetical source of error in the life tables, i.e. that the prefledging mortality in 1947 was unusually high, is almost certainly void. It was found that nearly 29 per cent of the eggs failed to hatch and about 48.5 per cent of the young died before fledging, resulting in 63.2 per cent mortality, or a net production of 0.92 fledglings per breeding pair (Paynter, 1949). This falls well within the range recorded at other Herring Gull colonies. For example, Paludan (1951) who admitted that his calculations are imprecise, estimated a production of 0.5 fledged young per pair, or 83 per cent prefledging mortality. In a study on the Summer Isles in the Irish Sea, Darling (1938) found five colonies (ranging from 6 to 150 individuals) which had prefledging mortality rates between 58.3 and 88.9 per cent, and which yielded from 0.78 to 0.96 fledged young per nest. Drost, Focke, and Freytag's (1961) German colony, which started with two pairs of birds and in 12 years built up to 139 pairs, had an average prefledging mortality rate of about 75 per cent, resulting in the fledging of an average of 0.7 gulls from each nest. On Skokholm, an island off the coast of Wales with a colony of 300 pairs of gulls, Lockley (1947) estimated that less than one fledgling per adult pair was produced. In another Welsh colony of 440 pairs, Harris (1964) reported a production of about one fledgling for each two nests.

Other species of gulls laying three-egg clutches show a similar range of nesting failures. A colony of Ring-billed Gulls (*L. delawarensis*) in Michigan suffered 88 per cent prefledging losses, producing 0.67 young per pair of adults (Emlen, 1956). The California Gull (*L. californicus*), in a colony in Utah, was found to have unusually low prefledging mortality, suffering a loss of only about 40 per cent of its eggs and young, and fledging 1.77 chicks per nest (Behle and Goates, 1957). In British Columbia a colony of Glaucous-winged Gulls (*L. glaucescens*), studied for two years, produced 1.0 and 1.7 young per nest, and had a mortality rate of 64 and 52 per cent, respectively (Vermeer, 1963). Four small colonies of Lesser Black-backed Gulls (*L. fuscus*) in the Summer Isles produced about 1.5 young from each nest, with a prefledging mortality rate of approximately 48 per cent (Darling, 1938).

In summary, the prefledging mortality rate at Kent Island in 1947 was below that which has been found in most other Herring Gull colonies and in a colony of *L. delawarensis*, and somewhat higher than that recorded for populations of *L. californicus*, *L. glaucescens*, and *L. fuscus*. From this it is concluded that the 1947 prefledging survival data are in the right order of magnitude and probably are not responsible for the failure of the composite life tables to indicate that the population was stable or increasing.

The third type of error that could distort the Kent Island life tables, causing the survival rates for breeding birds to appear too low to maintain the population, is a disproportionately high recovery of bands in early age classes. This could be brought about through some circumstance which allows young birds to be more readily recovered than older individuals, through a loss of bands among older birds which would reduce their rate of recovery, or through a combination of these factors. Both phenomena are difficult to detect but almost certainly at least one is the reason that the life tables are not reconcilable with the observed status of the population.

Paludan (1951, p. 111) believed that the mortality rate for the first year class of the Danish gulls was unrepresentatively high because newly fledged birds died near the natal colony, where they are more likely to be recovered and reported than older birds which range more widely. At Kent Island, however, the fledglings quickly leave the colony and winter far south of New Brunswick. Each successive year the length of the migration is lessened until as adults the birds winter only a few hundred miles from the colony (Gross, 1940). This migration pattern reduces the opportunity for any recoveries at Kent Island during the winter months. Moreover, the records indicate that very few immature gulls are recovered at the colony during any season. There seems no possibility that the recovery sample is biased in favor of immature birds because they die in the vicinity of the natal colony.

There remains to be considered the possibility that the wide dispersal of young birds during the winter, and their failure to return to the colony during the breeding season, might in some way enhance their chances of recovery over those of the less wide-ranging adults. If the immature gulls were in closer proximity than the adults to urban areas, where dead birds are more likely to be found, this possibility would exist. However, during the winter the younger birds are scattered from the heavily populated northeastern United States south to the more sparsely inhabited Gulf Coast and Central America, and in the breeding season return to the Northeast. On the other hand, the adults winter in the heavily populated Northeast and breed where observers are constantly alert for dead birds wearing bands. Bias in favor of the recovery of immature gulls seems improbable under these circumstances.

Having considered and rejected as improbable all other potential sources of error, we are left with only band loss to account for the discrepancies between the life tables and the observed status of the Kent Island colony.

All Kent Island gulls were marked with aluminum butt-end bands, rather than with the locking, clip-type bands now used in Europe. In a British study, using butt-end and clip bands on different samples plus supplementary durable plastic bands, Poulding (1954) found that during the first year after banding as fledglings, Herring Gulls with locking bands were recovered with twice the frequency of birds wearing butt-end bands. Breaking down the analysis further, it was noted that when the gulls wore butt-end bands only about four per cent of the year's total recoveries were made in the second half of the year, whereas nearly 41 per cent of the recoveries occurred in the second six months when the birds wore clip-type bands. Thus the data indicate that 50 per cent of the butt-end bands are lost in the first year and nearly all of this loss takes place before the bands are six months old. Observations of living birds confirmed the 50 per cent loss of butt-end bands and showed a complete retention of clip bands.

This evidence strongly suggests that the heavy initial loss of butt-end bands may be caused by the removal of the bands by the gulls, rather than by a weakening of the bands through wear. Differences in the strength of individual bands, and possibly variations in the manner of closing them, could well account for the rapid loss of half of the bands while some of those in the remaining half are retained in good condition for many years.

If this type of band loss occurs among Kent Island birds, the life tables would be significantly affected. It would mean, disregarding for the moment the normal reduction in the size of cohort caused by death, that at the time of fledging the banded sample would be twice the size it is when entering the second year of life. It follows that the number of recoveries in the second year, and all subsequent years, would be half of the total had there been no loss of bands and that the recoveries in the first year would be somewhat lower, but not a full 50 per cent lower because the bands are retained for part of the first half year. Viewed from a different aspect, recoveries in the first year would be disproportionately more numerous than those of the remaining year classes. The effect on the life table would be a reduction in the calculated number of birds surviving beyond the first year and, of course, a marked decrease in the apparent number of individuals which survive to the breeding age.

We have no evidence that Kent Island gulls lose half their bands during the first six months, but if we adjust the life table to compensate for such a loss and the table is then reconcilable with the apparent true status of the population, we shall have good circumstantial evidence that this is the source of error. If, for the sake of simplicity, we assume that the mortality rate is constant during the entire first year and that 50 per cent of the bands are lost at the end of the first six months and none in the second half year, one-third of the recoveries would occur in the second six-month period. Doubling this figure will give the number of recoveries which would have been made if the initial banded sample had been half its original size and there was no subsequent loss of bands. For the six combined cohorts there were 1,099 recoveries, 494 of which occurred during the first year. Making the proposed adjustments for the first year, the first year recoveries would drop to 329 and the total for the entire life span to 934.

Using these data to construct a new life table, it is found that the number of survivors reaching the breeding age of year 3-4 rises to about 116, versus 98.4 in the uncorrected table. The life expectancy at this age remains 3.3 years. With a breeding cohort of this size and with this life expectancy, a total of 477 eggs could be produced, which is an increase of 71 eggs over the total (406) calculated for the uncorrected life table. Nevertheless, this is still less than half the number required to maintain a level population.

If we were to assume that early band loss is the sole source of error in the life table, in order to achieve sufficient production at the breeding stage it would be necessary to adjust the recoveries in the first year so that their total would fall well below that of the second year. Such a low rate of mortality is obviously spurious. We must conclude that while early band loss is a distinct possibility in the Kent Island population, there must be additional losses later in the life span.

Band loss may fall into three broad patterns. The first, and the most expected, is loss which is correlated with the age of the bands. One would expect bands to become progressively weaker through wear and as a result be lost with increasing frequency. The second type is a proportional, or constant, loss. This is most likely to take place if the bands are continually removed by the birds or if they merely drop off at random. The third pattern, which may be uncommon, is an inconsistent, or fluctuating, loss. This may occur because of variations in behavior, such as shifts in feeding ranges from less saline to more saline water, which might have a variable effect on the durability of the bands, or because the new bands are not of uniform strength or are not all fastened securely. The large initial loss of bands noted by Poulding (1954) is an example of an inconsistent pattern which seems attributable to the latter cause.

If we are able to determine the pattern of band loss among Kent Island gulls it may then be possible, in certain instances, to adjust the raw data to compensate for the losses and to construct a life table which will document the colony's demography. Because the Kent Island birds were all marked with similar bands there is no control group against which the various cohorts may be tested, as in Poulding's study. We must, therefore, see if any evidence of band loss may be detected within the data available. Semi-logarithmic graphs of survivors (l_x) offer a means of approaching the problem.

If survivors (l_x) are plotted against age on a semi-logarithmic graph, the points will form a straight line if the rate of survival is constant. If the survival rate should decrease, or if there is an accelerating loss of bands which would create an apparent decrease in the rate of survival, the line will assume a sigmoid shape, being deflected downward. As may be seen in the plot for the six combined cohorts at Kent Island (Fig. 2), starting with the fourth year (year 3-4) of life, the survival rate is relatively constant for at least ten years (to year 12-13). There is then a downward trend, but there are so few recoveries one cannot be certain that the pattern is not an artifact. From this it is evident that if there is band loss that is correlated with age, it does not begin until sometime after age thirteen, by which time the cohort has dwindled to a small fraction of its initial size.

A further test for a correlation between a loss of bands and the time which they have been worn may be made by utilizing the recoveries of birds banded as adults. Between 1936 and 1947 a total of 1,856 gulls in adult plumage were banded; 97, or 5.2 per cent, were recovered up to 30 June 1963 (Table VIII).

TABLE VIII

Kent Island Adults Banded and Admissible[1] Recoveries

Year	Banded	Recoveries	Per cent
1936	200	2	1.00
1937	196	13	6.63
1938	611	46	7.53
1939	100	5	5.00
1941	155	5	3.23
1946	497	21	4.22
1947	97	5	5.15
Total	1,856	97	5.23

[1] See p. 493 for definition of admissible recoveries.

Nothing is known of the ages of these birds beyond the fact that they were in adult plumage and, therefore, were at least in their fourth year of life when banded. The maximum time available for recoveries from the youngest cohort is 16 years and from the oldest cohort it is 28 years. The oldest recovery was a bird banded 24 years earlier; the next oldest were two gulls which had borne their bands for 14 and 17 years, respectively. A semi-logarithmic survivorship curve for the 97 recoveries from the combined seven cohorts is shown in Figure 3. Owing to the paucity of older recoveries, no adjustment has been made for the fact that after age 16 the number of potential recoveries decreases because not all cohorts have been banded sufficiently long to yield recoveries between ages 17 and 24.

In Figure 3 a comparison is made between the semi-logarithmic survivorship curve for the birds banded as adults and the curve, starting at the fourth (adult) year, for those gulls banded as fledglings. If there is a positive correlation between the age of the bands and their loss, one would expect the survival rate for the latter group to decrease, and the curve to become deflected three years sooner than for the former group, because the birds banded as fledglings had borne their bands three years longer. If band loss begins during the first year following banding, the curves would diverge immediately. If it starts some years later the two lines would remain parallel until band loss begins, when the curve for the group with older bands would descend more rapidly; the plot for the group with the newer bands would continue in a straight line (a constant annual survival rate) for three additional years and then it too would begin to fall away.

As may be seen in Figure 3, the two curves remain nearly parallel for ten years, or in other words, until the group banded as fledglings has reached its thirteenth year. Then, as has been discussed, the curve for the group with the older bands begins to decline at a more rapid rate. This is not followed three years later by a decline in the other curve, which one would expect if bands began to be lost at an increasing rate after they had been worn thirteen years. In both groups, and particularly in the group banded as adults, there are so few recoveries in the older age categories it would be imprudent to attempt at this time to read any significance into these differences. All we may safely conclude is that if band loss is a function of age it almost certainly does not begin until the bands have been worn at least thirteen years. Because this means that the birds could have bred for ten seasons prior to the beginning of accelerated band loss, there seems little likelihood that this type of band loss would have a significant effect on the life tables.

This test also reveals an interesting fact regarding early band loss. It indicates that gulls banded as adults do not suffer a greater loss of bands in the first year than in later years, which is contrary to what one would have expected from Poulding's study (1954) of British fledglings. This is probably an indication that the North American butt-end bands are more uniformly durable than the British butt-end bands. This also seems to explain why the attempt to compensate for disproportionately

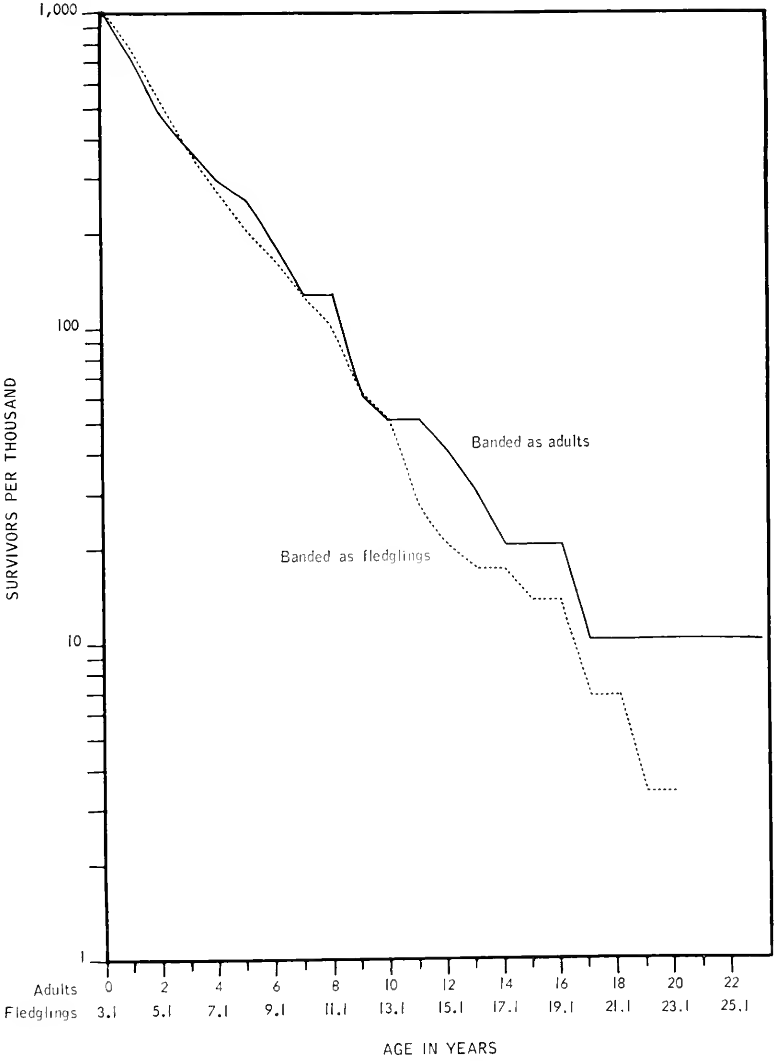

FIG. 3. Survivorship curves for Kent Island gulls banded as fledglings and as adults.

heavy band loss within the first year class of Kent Island gulls, banded as fledglings, failed to produce a satisfactory life table. Nevertheless, one could argue that adults do not remove their bands with as great a frequency as fledglings, explaining this difference by assuming that the legs of fledglings are more sensitive than those of adults and that the irritating bands are removed. Or, possibly, one could reason that in the process of learning to detect what is food, and what is not, the fledglings are attracted by the shiny bands and peck at them until they are loosened and lost. However, the fact that the Kent Island life table is not appreciably improved by adjustments made to compensate for heavier band loss in the first year of life seems to negate such arguments. The simple explanation that British butt-end bands are of more variable durability than those used at Kent Island seems the most satisfactory explanation.

The only pattern of band loss yet to be considered is that which occurs at a constant, i.e. proportional, rate. Having concluded that band loss is not positively correlated with the age of the band, and that bands are not lost with a greater frequency at any particular time during the bird's life, it is almost certain that the Kent Island population suffers a steady loss of bands during its entire life span. This would progressively reduce the number of recoveries in each successive age interval, thereby depressing the survivorship curve and reducing the calculated expectation of life throughout the life table.

We do not know the rate at which bands are lost and whether this rate is sufficiently low to allow at least a portion of the population to retain its bands until it has lived its full life span. However, because a living gull was found at Kent Island which had borne a band for 26 years, and because there are records from there of four birds which died between the ages of 20 and 24, it is evident that the rate of band loss must be comparatively low. For example, if the annual loss ran as high as 20 per cent, the roughly 32,000 individuals in the Kent Island sample would have dwindled to about 455 banded birds by the beginning of the twentieth year, even without considering attrition owing to mortality. If the average annual mortality were 10 per cent, making a cumulative annual reduction in the marked population of 30 per cent, there would have been just 37 banded survivors at the start of the twentieth year, certainly too few to have yielded five records of birds 20 years and older. Assuming that losses and mortality are each 10 per cent annually, there would be approximately 445 banded survivors after nineteen years, or about 1.4 per cent of the initial sample, which *seems* ample to allow for the recovery of five individuals in the next seven years. Although the Herring Gull is a long-lived species, 10 per cent average annual mortality would appear rather low; Drost et al. (1961) calculated a rate of 10 per cent for adult birds, but our calculations must include immatures within the average. If we continue to allow for 1.4 per cent survival at age 20, any increase in the mortality rate would have to be balanced by a decrease in the rate of band loss. Thus, 15 per cent annual mortality, which is about the figure found by Paludan for birds between the ages of 2 and 12, would mean a band loss of five per cent at the most. Crude as these calculations may be, it seems reasonable to conclude that Kent Island gulls lose bands at an average rate somewhere in the vicinity of 5 or 10 per cent per year and that the average annual mortality rate must range between 10 and 15 per cent.

These speculations are based on the premise that bands are recovered throughout the life span of the birds and are not totally lost before the oldest gulls die. There can be no proof that this is correct, but empirically it would seem that the oldest recoveries probably very nearly represent the potential natural longevity of the Kent Island Herring Gull. A larger cohort, more durable bands, and additional decades of observation surely would produce recoveries older than those now known, but it is difficult to imagine that these could be more than an insignificant fraction of the total sample.

CONCLUSIONS

It is now evident that a continued loss of bands accounts for the failure of the Kent Island life tables to reconcile with the observed status of the population (i.e. either a stable or increasing population). Unfortunately, in spite of our estimate that the loss amounts to about 5 or 10 per cent annually, there is no way by which the raw data may be adjusted to compensate for these losses. We know, for example, that there were 494 recoveries for the combined cohorts in the first nine-tenths of a year, and that without a ten per cent loss of the banded sample there would have been about 549 recoveries. In the second year there were 220 recoveries, but this number, without band losses during the second year, would have been approximately 243, plus an unknown number of individuals which lost bands in the first year but survived to die during the second year. The difference between the recorded recoveries and the number of recoveries there would have been had there been no band loss, increases, of course, in each successive age interval. This also has the effect of accelerating the descent of the survivorship curve and probably accounts for the difference between the Kent Island curve and that of the Danish population (Fig. 2).

From this analysis we must conclude that because of band losses the Kent Island banding records are nearly valueless as a means of investigating the dynamics of this population of Herring Gull. Their only use in studies of this sort, if one is willing to accept the premise that some bands are sufficiently durable to be retained through the life span of at least a few of the longest living gulls, is to demarcate the maximum potential longevity of the species. All North American Herring Gulls have been marked with similar butt-end bands, and band loss is without doubt the reason Hickey (1952) also failed in his attempt to construct an accurate life table. Because aluminum butt-end bands are used on almost all birds banded in North America, any data obtained from this source is suspect. Future workers should be particularly alert to the possibility of band loss before investing time and effort in this type of research.

Locking bands were used on nearly all gulls banded in Fenno-Scandia (Olsson, 1958). However, the material used in the manufacture of the bands evidently was not very durable, for Olsson estimated that about 5 per cent of their original weight was lost annually. Such rapid wear, and the resulting loss of bands, is presumably the reason for the apparent reduced maximum longevity of the Fenno-Scandian gulls when compared with North American and Danish birds. There can be little doubt that the similarity between the survivorship curves for Fenno-Scandian and North American birds is caused by band losses.

Paludan (1951) does not mention the type of band used on Danish gulls, but, according to Poulding (1954), butt-end bands were first used and later abandoned in favor of locking bands. Possibly some of the yearly variations in recovery rates that have been noted (p. 510) are attributable to changes in the type of bands employed. Nevertheless, this cannot be one of the main causes for these variations because one would expect the recovery rates for the more recent year classes to be consistently higher than those for the older year classes, but no such pattern is evident.

Band loss almost certainly occurred in the Danish population. Even if locking bands eliminate losses early in the life span, wear surely accounts for band failures in the later years of this long-lived gull. Bias in favor of recoveries during the first year of life, and band losses during the latter part of the life span, must be the primary reasons for the deficient Danish life table and its dissimilarity to other life tables. Fundamental differences between the mortality rates of the North American and Fenno-Scandian populations, on one hand, and the Danish population, on the other hand, as proposed by Paludan (1951) and Olsson (1958), seem most unlikely.

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SUMMARY

1. At Kent Island, New Brunswick, 31,694 Herring Gull (*Larus argentatus smithsonianus*) fledglings were banded with aluminum butt-end bands between 1934 and 1939; by 30 June 1963 there were 1,099 (3.47 per cent) recoveries suitable for use in a mortality series (Table I).

2. The maximum potential age for a recovery in the oldest cohort is 28 years, and in the youngest cohort it is 23 years; the two oldest birds at death were in their twenty-fourth and twenty-second years; one gull was captured alive in its twenty-sixth year.

3. About five per cent of all recoveries are of birds which have been shot; rates vary within the six year classes from 3.6 to 6.5 per cent; probably more birds are shot than are reported because the species is protected by law; no gull older than thirteen has been reported shot; there is no indication that immature birds are more readily shot than adults.

4. Using prefledging mortality data for 1947 (Paynter, 1949), composite life tables are constructed for each of the six cohorts and for the combined cohorts (Table II); survivorship curves

are also drawn (Figs. 1 and 2); there are minor yearly variations, but the patterns are generally similar, showing heavy mortality the first year, lessened mortality the second year, and a lower, relatively constant, rate thereafter.

5. Assuming breeding begins in the fourth year (year 3-4), that the average clutch is 2.5 eggs, and that each nesting results in the production of 0.92 fledglings (Paynter, 1949), it is found that an average of about 98.4 gulls attain breeding age from each 1,000 eggs laid, and these have a life expectancy of 3.3 years, enabling them to produce 405.9 eggs, or about 41 per cent of the number required to maintain a stable population.

6. The population is believed to have been stable, or possibly expanding, from at least 1935 to 1948. The life tables must, therefore, be faulty.

7. Three types of error leading to distorted life tables are possible: 1. recoveries were accumulated for too short a period (23 to 28 years) to document the potential life span; this is probably a minor and insignificant source of error. 2. The 1947 egg and prefledging mortality rates were excessively high; this is rejected because comparable rates have been found in this and related species. 3. There is a disproportionately high recovery of bands in the early age classes because (a) young birds are more readily recovered, (b) older birds lose bands and are lost from the sample, or (c) both factors are operative.

8. It is certain that band loss, resulting in a disproportionately high recovery of young birds, must account for the failure of the life tables to document the demography of the Kent Island population.

9. Band loss could be (a) positively correlated with the age of the band, (b) proportional (i.e. constant) with respect to the size of the sample, or (c) fluctuating; it is concluded that bands are lost at a relatively constant rate throughout the life span.

10. Assuming that some bands are retained long enough to document the maximum potential life span, mortality and band loss combined seem not to exceed 20 per cent annually; it is suggested that band loss averages around 5 or 10 per cent per year and that the average annual mortality ranges between 10 and 15 per cent.

11. Hickey's (1952) life table (Table III; Fig. 2) for North American gulls proved faulty presumably because of band losses similar to those at Kent Island.

12. Olsson's (1958) life table (Table VI; Fig. 2) for Fenno-Scandian gulls is similar in pattern to those for North America

and Kent Island; locking bands probably eliminated losses through mechanical failure, but rapid wear (five per cent annually) doubtless resulted in band loss correlated with age and eventually to a total loss of marked birds by the eighteenth year, foreshortening the apparent maximum life span.

13. Paludan's (1951) life table (Table V; Fig. 2) for Danish gulls, with its higher survival rate, most nearly fits what is known of the demography of the species but bias in favor of recoveries during the first year, wide variations (of unknown cause) in yearly recovery rates, and probably band losses toward the end of the life span distort the data.

14. Suggestions of essential differences between the mortality rates of the various populations are considered spurious.

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